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SCHIZOCHROAL EYES AND VISION OF SOME SILURIAN ACASTID TRILOBITES

by E. N. K. CLARKSON

ABSTRACT. The eyes of some British Silurian Acastinae are described and analysed functionally. Techniques are given for measuring the size and spatial arrangement of the lenses of schizochroal eyes and the angular bearings of their lens-axes, from which may be inferred the angular range of vision of the whole eye and the relative visual acuity in different directions. In the post-larval ontogeny of the eye of *Acaste downingiae* (Salter) the lens-number increases with size but the angular extent of the visual field remains constant. Two eye-variants are distinguished and attributed tentatively to sexual dimorphism. Comparisons are made with the adult eyes of *Acaste downingiae macrops* (Salter) and *Acastoides constricta* (Salter).

Variation of lens-size and strong differentiation between the relative acuity in the horizontal and vertical directions of vision are perhaps the most significant features of the eyes of Acastinae, and the latter is interpreted as indicative of movement-perceiving eyes. Analogies are made with the compound eyes of recent arthropods, and the ecological significance of the work is briefly discussed.

TRILOBITES are amongst the earliest arthropoda to appear in the geological record and are the oldest fossil animals known to have possessed compound eyes. The morphological similarity between the eyes of trilobites and those of other arthropods was noted by the first students of trilobite morphology, including Quenstedt (1837) and Burmeister (1846). Since then, trilobite eyes have been studied in detail by many workers; in particular Barrande (1852), Clarke (1889), Lindstrom (1901), Brink (1951), and Beckmann (1951). An excellent summary of current knowledge is given by Harrington (1959) in the *Treatise on Invertebrate Paleontology* Part O (Arthropoda I), pp. O 87–O 92. In the main these workers have contributed to our knowledge of the morphology and development of trilobite eyes, and there has been little attempt to relate structure to function.

I have made a functional study of the eyes of a number of species of trilobites. This paper presents the results of the first part of this investigation and concerns a small group of trilobites which have proved especially suitable for such functional analysis.

Within the Trilobita there are two distinct types of eyes, defined by Clarke (1889) as 'holochroal' and 'schizochroal'. Full descriptions of the two types are given by Harrington, and it is sufficient to state here that holochroal eyes consist of many small closely packed lenses overlaid by a single corneal membrane, through which the lenses may usually be seen. Schizochroal eyes have a fairly small number of relatively larger lenses, the maximum number recorded being 770 (Roy 1933). Each lens has its own cornea, and is separated by interstitial material from its neighbours. Whereas holochroal eyes are present in trilobites of all ages from Lower Cambrian to Middle Permian, schizochroal eyes, which are to be found only in the Phacopina, a few Cheirurina and, possibly, Harpina, do not occur before the Ordovician or after the Devonian. They are consequently to be regarded either as a specialized development of the normal holochroal pattern or as quite distinct organs of independent origin. As yet it is not known which of the two possibilities is the more probable. The suborder Phacopina, in which only schizochroal eyes occur, appeared in the early Ordovician after the main

lines of trilobite descent had been established (Stubblefield 1959), and reached its acme comparatively late in the history of the Trilobita when the class as a whole was declining.

Schizochroal eyes of Phacopina have been found to be particularly suitable for use in the investigation of the nature of trilobite vision because of their large size and few lenses. Several species of Phacopina are common in the English Wenlock Limestone (Silurian); amongst them are Acastinae in a state of preservation suitable for study. These are described in this paper.

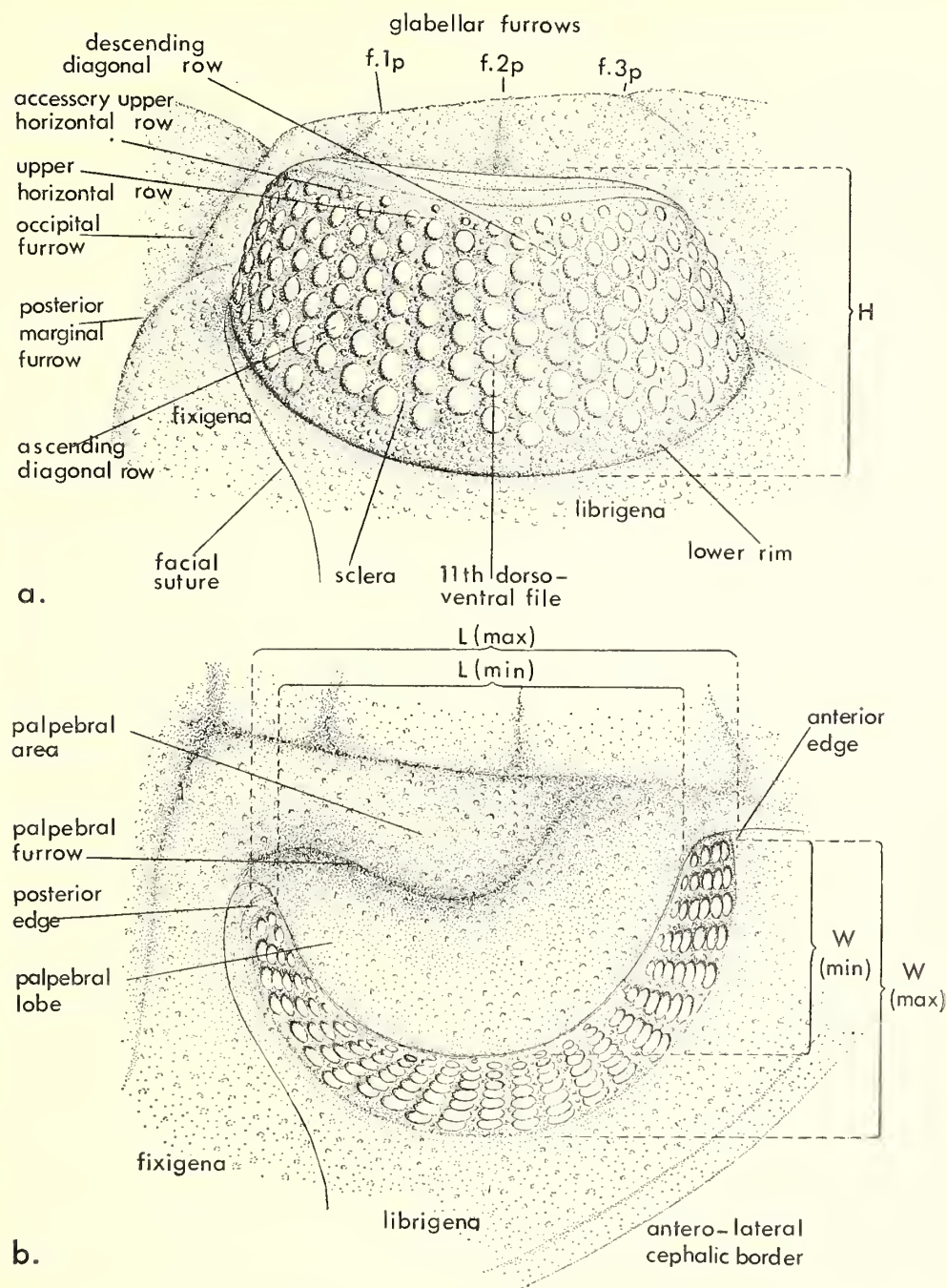
TERMINOLOGY

The eyes of Phacopina have been frequently figured and Lindstrom's (1901) magnificent monograph contains figures of some of these eyes in thin section. Their detailed morphology has seldom been described. In the succeeding text descriptions, although the terminology of the *Treatise* following Warburg (1925) has been used, it has been necessary to supplement this with a number of new terms.

These terms, illustrated in text-fig. 1, are applicable to the eyes of *Acaste* and all other Phacopina. The external surface of the eye which bears the lenses and is bounded by the facial suture is known as the '*visual surface*'. The limits of the visual surface nearest to the sagittal line are defined as the '*anterior*' and '*posterior edges*'. The '*interlensar sclera*', defined by Clarke (1889), is that part of the visual surface which lies between the schizochroal lenses and is not covered by cornea. It is generally identical in structure with the rest of the cephalic exoskeleton.

All the lenses are invariably arranged conspicuously in hexagonal close packing and thus form three intersecting rows, defined as the '*dorso-ventral files*' and the '*ascending*' and '*descending diagonal rows*'. The former term is intended to replace the somewhat misleading expression 'vertical rows', as these files usually diverge ventrally and are not always vertical. Since the dorso-ventral files are more frequently referred to in the text than the other rows, the term '*file*' by itself is normally used to distinguish them. The files are numbered 1, 2, 3, . . . etc., from the anterior edge of the eye. Lenses occur in alternate files at the same level from the front to the rear of the visual surface, and lie in '*horizontal rows*'. The '*upper horizontal row*' is defined as that which extends the full distance below the facial suture. Within this row the central lenses are always smaller than the outer ones. In *Acaste* and other Phacopina there is often an '*accessory upper horizontal row*' lying above the latter. It is confined to the posterior part of the visual surface and generally consists of a few lenses only. In some cases the regularity of the pattern in which the lenses are distributed is disrupted by the interpolation of one or two extra lenses between certain files. The files on either side of these extra lenses are usually bowed outwards, but a short distance from the hiatus all the files are quite straight and normal in appearance. This condition has been observed in a small specimen of *Acaste downingiae* s. str. (Salter), SM A 28744 (text-fig. 4a, b, Pl. 1, figs. 1, 4, 5).

Discussion of the angular relationships of the lens-axes involves the use of the terms '*longitudinal*' and '*latitudinal axial angles*' which refer to the measurable angles of separation between the axes of adjacent lenses. Since the lenses in two neighbouring files are situated at different levels and hence usually have incongruent latitudinal bearings, the longitudinal axial angles are taken as half the angle between the axis of any one



TEXT-FIG. 1. *Acaste downingiae* (Salter) s. str. External morphology of eye and immediate environs, After SM A 28720 (eye-variant A); *a.* Lateral view. *b.* Dorsal view. Dimensions; L, W, H, length, width, height.

lens and that of the lens in the same horizontal row (i.e. at the same level) in the next file but one. A latitudinal axial angle is the angle of separation between the axis of any lens and that of the lens directly above or below it in the same dorso-ventral file.

The term '*facet*' which has sometimes been substituted for '*lens*' is not used here since it has already been applied in trilobite terminology to designate the articulating antero-lateral part of the thoracic pleurae in trilobites capable of enrolment.

TECHNIQUE OF INVESTIGATION

A simple apparatus was devised in order to measure accurately the angular bearings of the individual lenses of schizochroal eyes. A set of such measurements of all the lenses of one eye, when plotted graphically, gives the total angular range of vision, and the angular separations between the lens-axes. This apparatus was also used for a detailed study of the sizes and the spatial arrangement of these lenses, and their mode of development during postlarval ontogeny.

Apparatus. The apparatus (text-fig. 2) consists of two units: a stereoscopic microscope fitted to a long arm stand, allowing the optical assembly to be either horizontal or vertical, and a turntable. (The microscope illustrated is by W. R. Prior & Co. Ltd.) The specimen selected for analysis is fixed firmly on the horizontal turntable, which can be rotated so that different parts of the visual surface of the eye may be examined in turn.

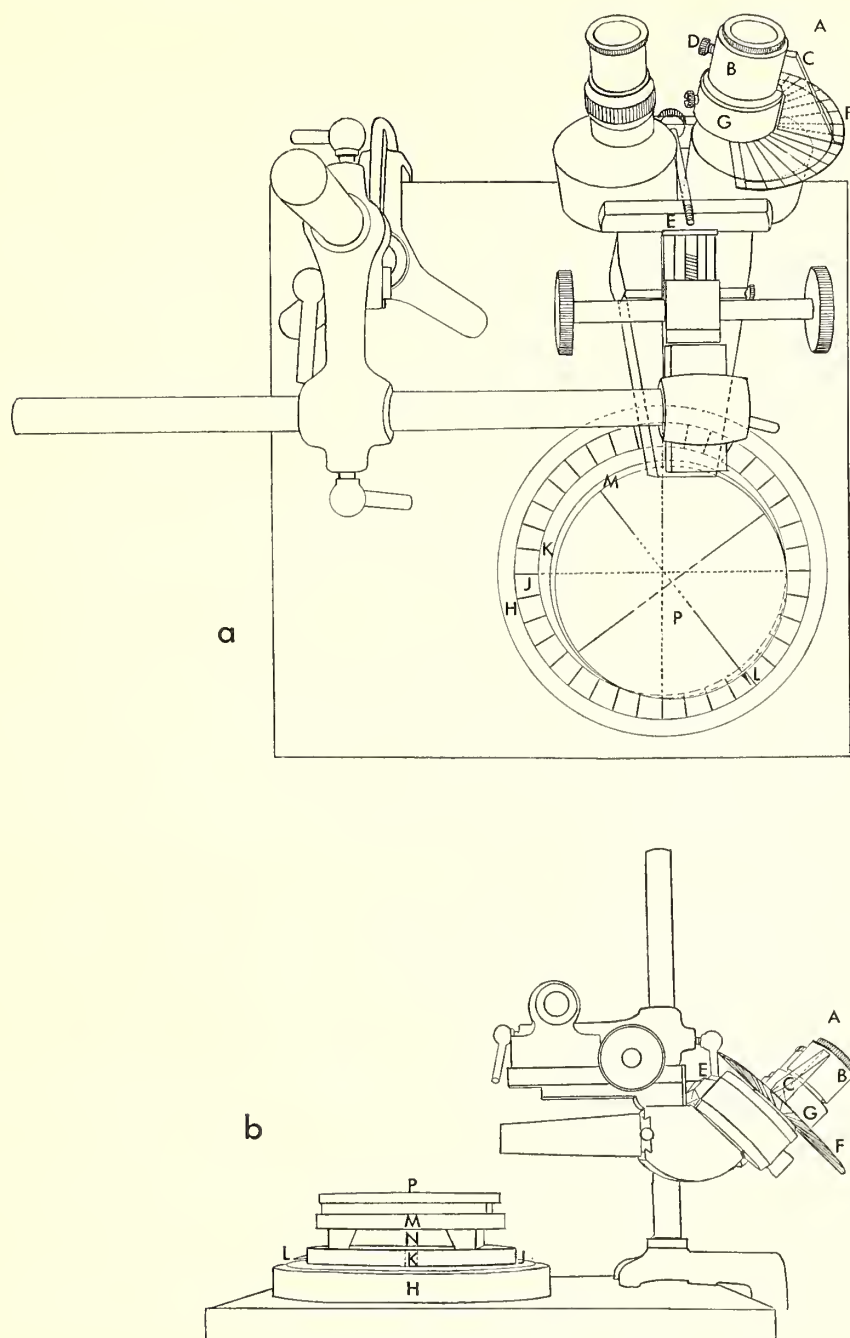
The optical system used has a maximum magnification of $\times 40$. The left eyepiece (A) may be fitted either with a micrometer scale registering to $\frac{1}{10}$ mm. for measurement of lens diameters and spacing, or with interchangeable graticules ruled in 0.5 mm. or 0.25 mm. squares. An aluminium collar (B) with its pointer (C) was fitted to the left eyepiece. This can be locked by the screw (D). In determining the angular bearings of the lens-axes the pointer (C) is aligned parallel with one of the sets of lines on the graticule. The whole eyepiece assembly complete with collar and pointer may be rotated inside its barrel. An immovable protractor (F) is held by a Perspex collar (G) on the barrel of the eye-piece below the aluminium collar. The 90° bearing of the protractor is fixed horizontally, and upon rotation of the eyepiece assembly any angle measured by means of the graticule will be shown by the pointer (C) on the protractor. To avoid rotation of the graticule during measurement the eyepieces have been adjusted for personal eye-spacing. They are locked by means of the clamp (E).

The rigid turntable consists of an immovable 6½ in. wooden disc (H) on which is fixed a 6-in. circular protractor (J). Above the protractor is a rotating upper assembly of Perspex. This consists of three graduated discs, of which the lowermost (K) is the largest, and has a pointer (L) bearing on the protractor (J). This disc rotates about a central screw, and has on its upper surface two parallel bars grooved so that the dovetailed fixture (N) of the base of the next disc (M) may slide between them. This disc (M) carries on its upper surface another dovetailed fixture at right angles to that on the lower surface, engaging with grooved bars on the lower surface of the uppermost disc (P). The plane surface of the top disc (P) is inscribed with two sets of lines at right angles, one parallel to the pointer (L), the other perpendicular to it. If the specimen is mounted in plasticine on the upper disc, either of its eyes may be brought into the field of view of the microscope by sliding the discs, and held level whilst the stage is rotated.

Orientation of the trilobite. All measurements of the angular bearing of the lens-axes are made with primary reference to the trilobite's plane of bilateral symmetry, the sagittal line. This line is orientated parallel with one of the lines engraved upon the upper surface of the disc (P), so that its bearing can be measured on the protractor (J) by means of the pointer (L).

The chief problem arises in the orientation of the cephalon in profile, i.e. with respect to the horizontal plane of the apparatus. A conventional 'horizontal' orientation has been chosen which probably approximates to the original attitude of the cephalon as it was in life (p. 27). This orientation is defined as that in which the upper edge of the visual field, or at least the greater part of it, lies along a single latitude. In this attitude the 'horizontal' rows of lenses in the eye are in fact aligned horizontally, a feature which may be used in practice as a guide to the orientation of the specimen on the stage.

Size and spacing of lenses. It is desirable to make a graphical representation of the whole visual surface, in order to show the number, size, and spacing of the lenses in every file, and to trace their ontogenetic



TEXT-FIG. 2. Apparatus used in the investigation of vision in trilobites. *a*, *b*, perspective views from top and side. Explanation in the text.

development and intraspecific variation. Although Barrande (1852, p. 514) had drawn up a table showing intraspecific variation in the number of lenses per file in *Phacops secundus* Barrande, Clarke (1889), working with *Phacops rana* (Green), was the first to attempt to show diagrammatically the number and arrangement of the lenses. He represented each lens as a dot equidistant from its neighbours. The dorso-ventral files were shown as vertical, and the diagonal rows as inclined at 60° to the vertical. Beckmann (1951) used a similar method, but showed the diameters of the lenses with greater accuracy. Although this projection can give an accurate representation of the sizes of the lenses it necessarily distorts their relative positions.

The problem, as in cartography, is to find an appropriate projection which will depict a portion of an approximately spherical surface with minimal distortion. The projection chosen resembles a conical equidistant projection in character though not in method of construction. This projection (text-fig. 4) shows both the spacing of the lenses and their diameters with relatively little distortion. The method of construction used is as follows (text-fig. 3). A long central file (A) is selected and observed in profile; the distances between the lens centres may then be measured accurately by the eyepiece micrometer and plotted on paper at an appropriate magnification (text-fig. 3c). The specimen is then turned so that the visual surface is perpendicular to the observer, and the distances between the lens-centres of adjacent files are measured by triangulation from the lenses of the marked file A whose positions have already been recorded.

The lenses of files B and C are normally at equal distances from those of file A and one set of measurements will therefore suffice for both. The positions of the lens-centres of further files are then plotted in the same way giving a grid for all the lens-centres. Slight irregularities in spacing often occur near the anterior and posterior edges of the visual surface and in such cases separate measurements must be made for the spacing of each lens. When the grid is complete the measured diameters of all the lenses may be drawn in.

Angular bearings of the lens-axes. Before measuring the angular bearings of the lens-axes, the eyes are lightly coated with ammonium chloride and are illuminated against a dark background. The longitudinal and latitudinal components of the angular bearings of each lens are measured separately.

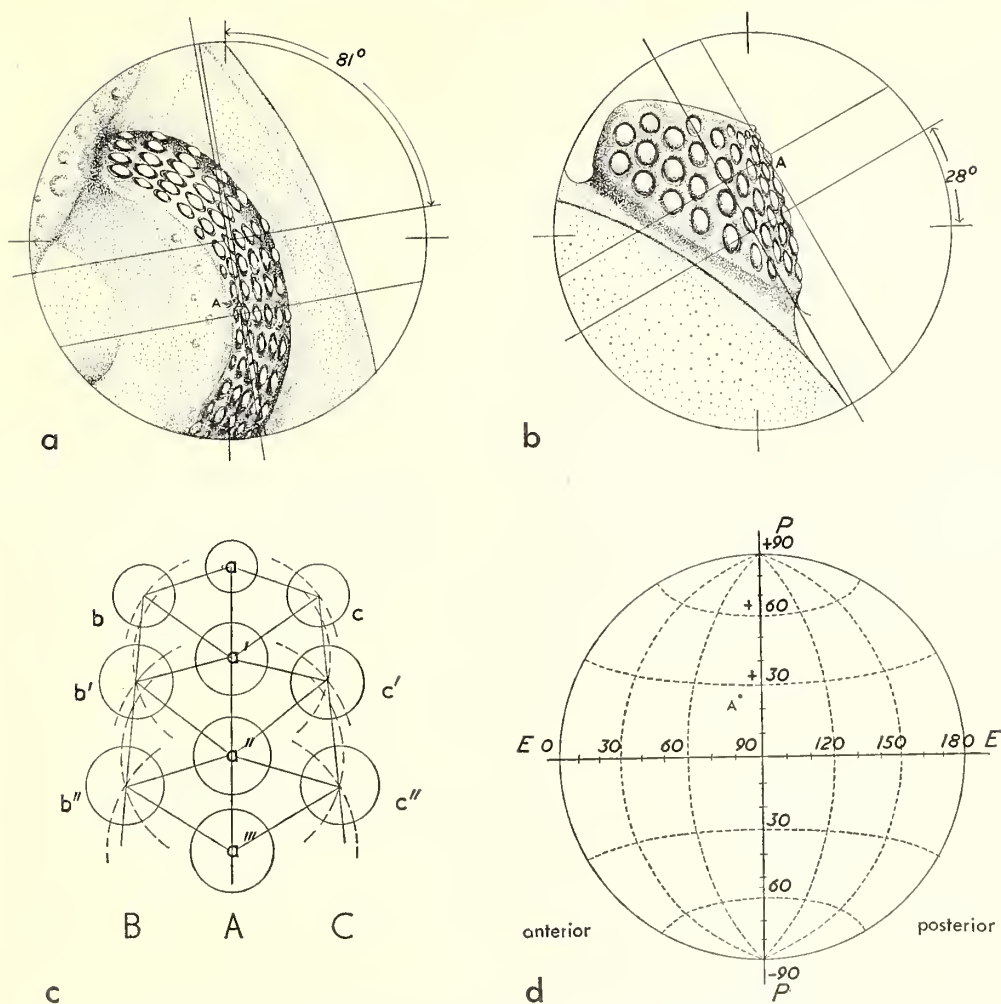
The longitudinal component is measured with the microscope vertical so that the eye is seen directly from above (text-fig. 3a). The left eyepiece assembly with its pointer (C) is rotated in its fixed barrel until the set of lines on the graticule parallel with the pointer has the same angular bearing as the axis of the lens. The other set of lines on the graticule are now parallel with the principal plane of the lens. The pointer now records the longitudinal component on the protractor (F). Each lens is examined in turn by this method.

The microscope body is restored to the horizontal position (text-fig. 2), in order that the latitudinal components may be measured. For each lens, the turntable is rotated so that the pointer (L) shows the already recorded longitudinal bearing of the particular lens under investigation and its profile may be observed through the microscope as it projects from the curving surface of the eye (text-fig. 3b). The graticule is then used for the determination of the latitudinal bearing of this and other lenses in the manner already shown.

All the dorso-ventral files are brought into view in turn for study but with continued rotation of the turntable, either the glabella or the high posterior border may move into the field of view and obscure the lenses of the first or the last few files. The turntable is then reversed through 180° , and the lenses are measured from the opposite direction.

In both sets of measurements, the close spacing of the lines in the graticule ensures considerable accuracy. Repeated measurements on the same eye have shown that the margin of error is generally less than 1° and never more than 2° . The ease of measurement with which this degree of accuracy can be attained depends, however, on the detailed morphology of the lenses and the sclera.

In *Acaste* the individual lenses project above the surface of the interlensar sclera, and the junction between lens and sclera is normally very distinct (text-fig. 1). In some other Phacopina, and particularly in *Phacops* s.s. (text-fig. 3a, b) the sclera may be highly inflated so that each lens appears sunken in a shallow crater-like depression. When one of these lenses is seen directly in profile, the lens/sclera junction may be just obscured by the inflated sclera. The uppermost lenses may, furthermore, be set obliquely to the surface of the sclera, and the lower rims of the depressions in which they lie may be more strongly pronounced than the upper rims. All the axes of such lenses in consequence have a lower

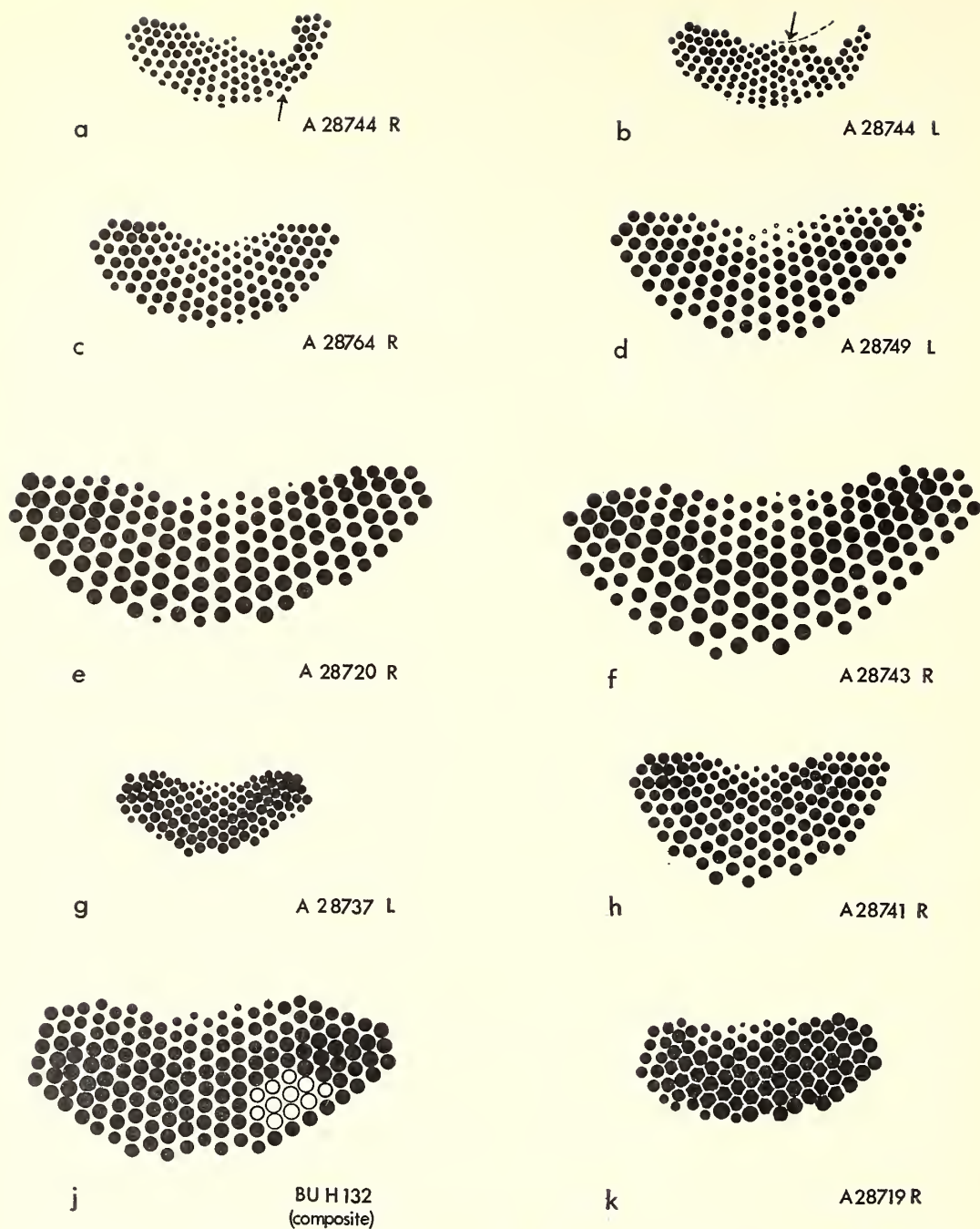


TEXT-FIG. 3. Technique of measurement of the spatial and angular relationships of the lenses. *a*, *b*, Angular directions of lens-axes of *Phacops latifrons* Bronn. The two sets of perpendicular lines represent the central cross wires of the graticule, and parallel lines following the optic axis and principal plane of the lens. Other graticular lines have been omitted for clarity. Lens A has latitudinal and longitudinal axial bearings of 28° and 81° respectively; *c*, Triangulation of lens-centres in files B and C from those of file A; *d*, Lambert equal-area net with notation adopted for recording bearings of lens-axes. The bearing of the axis of lens A (*vide* text-fig. 3*a* and *b*) is indicated.

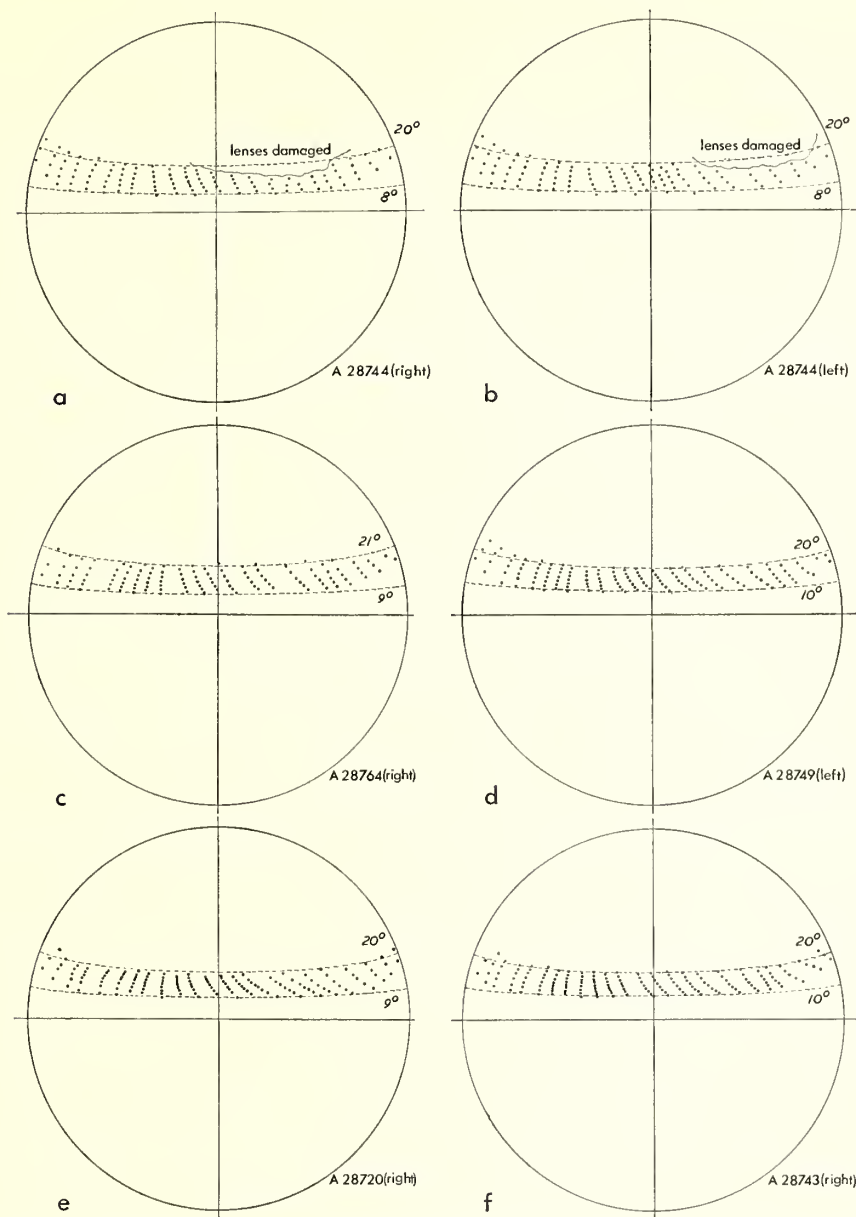
latitudinal elevation than if they had been set flush with the surface, with their principal planes parallel with the outside of the sclera. In making accurate estimations of the latitudinal bearing of such lens-axes, the lens must be kept in focus as it is being rotated into position for measurement.

When the longitudinal and latitudinal components have been measured, the resultant bearings of all the lens axes are plotted upon a Lambert equal-area stereographic net (text-figs. 5, 6). Text-fig. 3*d*, shows the notation adopted in the description of the axial bearings of the lenses.

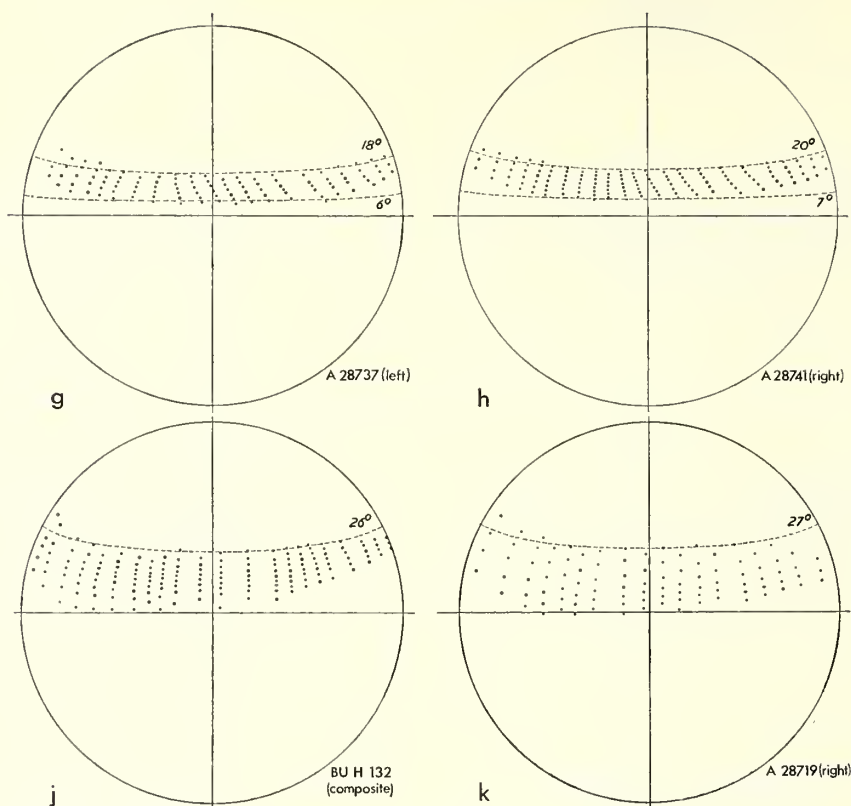
The term 'visual field' is used here to include the area enclosed by the peripheral lens-axes. As each individual ommatidium presumably had a certain visual field of its own, however, the actual field of



TEXT-FIG. 4. Projected visual surfaces of Acastinae. All $\times 10$. *a-f*, *Acaste downingiae* (Salter) s. str., eye-variant A; *g-h*, *A. downingiae* s. str., eye-variant B; *j*, *Acaste downingiae macrops* (Salter), composite figure from both eyes. The blank circles represent badly weathered lenses; *k*, *Acastoides constricta* (Salter). The anterior edge is at the left-hand side in all these diagrams. Thus right eyes (R) are viewed from within; left eyes (L) from outside. In SM A 28744 the visual surfaces are slightly damaged. Irregularities in lens-distribution are marked by arrows.



TEXT-FIG. 5. Visual fields and axial bearings of lenses shown by stereographic projection. *a-f*, *Acaste downingiae* (Salter) s. str., eye-variant A.



TEXT-FIG. 6. Visual fields and axial bearings of lenses (cf. text-fig. 5) *g, h, Acaste downingiae* (Salter) s. str., eye-variant B. *j, Acaste downingiae macrops* (Salter), composite figure from both eyes; *k, Acastoides constricta* (Salter).

view of the trilobite eye as a whole probably extended some way outside the visual field shown on the stereogram (p. 25). The term is retained for convenience of description.

FUNCTIONAL DESCRIPTIONS OF THE EYES OF ACASTINAE

Acaste downingiae (Murchison 1839)

This species occurs in the Wenlock Limestone (Silurian) of Dudley and the Welsh Borderland. Murchison's original description (1839, p. 655, pl. 14) is very brief, and the fullest existing accounts of the species are those of Salter (1853, 1864) in which six varieties are enumerated. In the definition of these varieties, Salter used various morphological criteria, including the external structure of the eye, which, as he observed, varies considerably within the species. Although the following detailed studies of the eyes of *A. downingiae* have given further information which might be of some taxonomic value, it is not the purpose of this paper to attempt any further systematic interpretation of the species, and Salter's varieties, as revised by the Richters (1954), are retained,

pending taxonomic revision of *A. downingiae* and related species by Shergold which is now in press (personal communication).

The exoskeleton of this species appears to have been remarkably resistant to pressure, as compared with some other Wenlockian Phacopina and Cheirurina which are frequently found to be crushed. Hence 40 out of the 62 specimens of '*A. downingiae*' in the Sedgwick Museum, with cephala ranging in length from 3.5 mm. to 11 mm., are almost perfectly preserved and show no trace of distortion. Most of the very best specimens are enrolled and a few are partially silicified. Extremely small, though crushed, specimens are known and in some of these the lenses can be distinguished.

Almost all the Sedgwick Museum specimens have been identified as *A. downingiae* s. str. (Salter). Of Salter's other varieties, no material showing intact eyes of *A. downingiae inflatus* (Salter), *A. downingiae cuneatus* (Salter) or of *Acastella spinosa* (Salter) has been available for examination. A single almost perfect specimen of *A. downingiae macrops* (Salter) with well-preserved eyes was lent by the Geology Department of Birmingham University and two specimens of *Acastoides constricta* (Salter) were in the Sedgwick Museum collection. These latter species are described in a later section of this paper.

Acaste downingiae (Salter 1864) s. str.

Plates 1, 2; Plate 3, figs. 1-3.

1839 *Calymene* ? *downingiae* Murchison, p. 655, pl. 14, fig. 3a.

1851 *Phacops downingiae* (Murch. sp.); M'Coy, p. 160.

1853 *Phacops downingiae* Murchison; Salter, p. 1-12, pl. 1, figs. 1, 2, 5-13, 15.

1864 *Phacops (Acaste) downingiae* Murchison, var. α *vulgaris* Salter, p. 26, pl. 2, figs. 17-25.

1954 *Acaste (Acaste) downingiae* (Murchison 1839); R. and E. Richter, pp. 16-17, pl. 3, figs. 36-41.

A comparison of Salter's descriptions and figures with the Sedgwick Museum specimens indicates that within Salter's 'variety' there are at least two distinct forms differing in the size and position of the eye, the character of the visual surface, the degree of inflation of the glabella, and the character of the genal angles.

The eyes of the two forms which he figured are quite distinct and do not have any morphological intermediates. About three-quarters of the fully grown Sedgwick Museum specimens have large eyes with more widely spaced lenses and rounded genal angles as in Plate 1, fig. 8 (cf. Salter 1853, fig. 1). This form will be termed eye-variant A. The rest of the specimens have smaller eyes with more closely spaced lenses and pointed genal angles (ibid. fig. 2) and are referred to as eye-variant B. The two types of eye also differ in the number and arrangement of the lenses within the visual surface.

The existence of two eye-variants, which are often associated with minor morphological differences in the cephalon, has also been detected in *Phacops rana* (Green), *P. latifrons* (Bronn), *P. breviceps* Barrande, and *P. fecundus* Barrande by the present author.

In *Acaste downingiae* s. str. five fully preserved specimens of eye-variant A (SM A 28744, -64, -49, -20, and -43) and two of eye-variant B (SM A 28737, -41) have been selected for analysis as representative examples of individuals of different sizes. Comparisons were made throughout with other specimens of equivalent dimensions. In each eye-variant specimens of the same size normally have a very similar number of lenses.

Eye-Variant A. Text-figs. 1*a*, *b*; 4*a-f*; 5*a-f*; 7*a-e*; 9*a-e*; Plate 1, figs. 1-9; 2, figs. 1-4; 3, figs. 1-3.

Eyes of moderate size, not particularly prominent, occupying the central third of the cephalic length (sag), and extending from glabellar furrow 3p almost to the posterior marginal furrow. The anterior edge almost reaches the axial furrow, but the posterior edge is free and lies further from the sagittal line. In profile (Pl. 3, fig. 1) the eye-base lies about half way between the genal angle and the crown of the glabella, but the palpebral lobe does not quite reach the level of the latter. Curvature of visual surface in dorsal aspect quite strong, profile curvature extremely low (text-fig. 1, Pl. 1, fig. 8). The visual surface rises abruptly from an indistinct eye-platform, is bounded ventrally by a shallow groove, and projects slightly laterally. Both the upper and lower eye borders are parallel in young specimens but in older ones the lower border is downwardly convex. Palpebral lobe granulated, consisting of a narrow flattened outer strip running parallel with the facial suture, and sloping first gently, then steeply to the palpebral furrow. In some specimens a narrow line of shallow pits can be seen near the outer rim of the palpebral lobe running parallel with the facial suture (Pl. 2, fig. 3). Palpebral area very granular, shelving gently towards the axial furrow, open posteriorly.

Lenses (see Table 1) normally disposed regularly in 22-24 files, but in the smallest specimen (SM A 28744. Text-fig. 4*a-b*, 5*a-b*, 7*a-b*) there are two extra lenses in the right eye and a hiatus in the centre of the left eye, which breaks up the regularity of the visual surface. Such irregularities are uncommon. In the smallest specimen the angle at which the files diverge ventrally is high, but in the largest specimens some of the central files are subparallel. The lenses of small specimens are almost uniform in size (Table II and text-fig. 9) and spaced at about the distance of a lensar radius from each other (cf. Salter 1853, pl. 1, fig. 8). Subsequently, size differentiation appears, and in the larger specimens the upper central region of the visual surface contains small lenses lying between the horns of a crescent of larger lenses which increase in diameter downwards. At the lower ends of the diagonal rows, the lenses are often small and immature. In SM A 28744 (text-fig. 4*a-b*) the lowest lenses are elliptical and set close in under the lenses above them, but in larger specimens the corresponding lenses are never elliptical. An accessory upper horizontal row is usually present, extending posteriorly from about the centre of the eye.

The interlensar sclera may be flat or slightly inflated, and is covered with minute granules. Ventrally they become continuous with the granules of the lower rim of the visual surface.

EXPLANATION OF PLATE I

Acaste downingiae Salter, s. str. Eye-variant A. Wenlock Limestone, Silurian. Dudley, England.

Figs. 1, 2, 4, 5, 7. Small specimen, SM A 28744. Right eye, lateral aspect, $\times 20$. 2. From above, $\times 5$. 4, 5, 7. Right eye, lateral aspect, $\times 20$.

Figs. 3, 6. SM A 28749. Left eye, lateral and dorsal aspects, $\times 7.5$. In fig. 6 the eye of a neighbouring specimen of the same species is visible on the left-hand side.

Fig. 8. SM A 28764. Right eye, lateral aspect, $\times 15$.

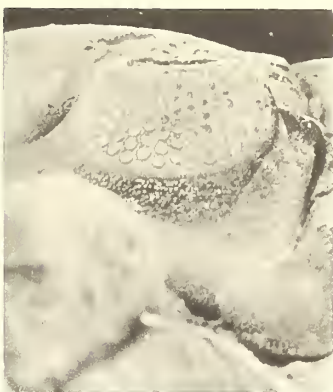
Fig. 9. SM A 28720. Lenses near lower rim of right eye, $\times 25$.



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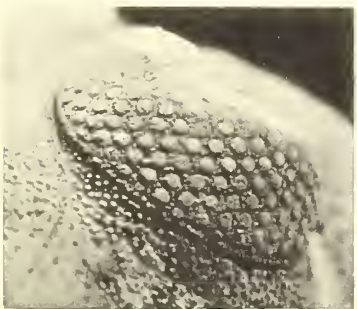
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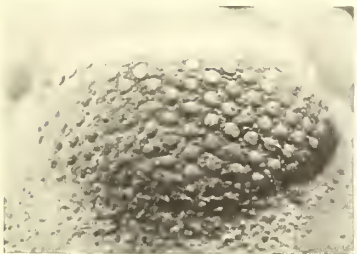
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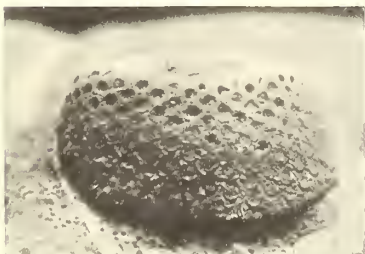
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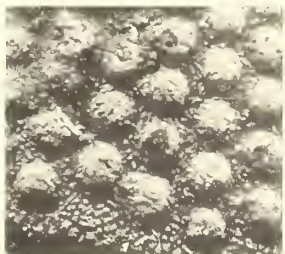
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Eye-variant B. Text-figs. 4g, h; 6g, h; 8a-b; 9f, g; Plate 2, figs. 5-8.

Eyes smaller than in eye-variant A, situated more towards the rear of the cephalon and not reaching anteriorly quite as far as glabellar furrow 3p. Palpebral lobe more highly inflated than that of eye-variant A, curving uniformly downwards to the axial furrow, with less trace of a palpebral furrow. Similar shallow pits to those seen in eye-

TABLE 1—Distribution of lenses
Acaste downingiae (Salter) s. str.

Eye-variant A

Specimen	Number of lenses per file (front to rear)								Total	Max. per file
SM A 28744 (Rt)*	345	666	667	677	555	4 (2) 33	334	32	111	7
SM A 28744 (Rt)†	345	666	667	677	676	6 (2) 66	554	32	127?	7
SM A 28744 (Lt)*	345	666	667	677	7 (5) 66	654	333	22	121	7
SM A 28744 (Lt)†	345	666	667	677	7 (5) 66	666	554	32	130?	7
SM A 28764	345	666	767	676	776	766	543	2	122	7
SM A 28749	345	677	778	788	888	766	654	3	138	8
SM A 28720	345	677	777	787	777	767	665	43	140	8
SM A 28743	1456	788	889	889	888	877	665	43	159	9

N.B. In SM A 28744 the upper posterior parts of both eyes are slightly damaged.

* Number of lenses actually preserved. † Probable original number. () Small extra lenses interpolated between complete files and breaking up the regularity of the visual surface (p. 12).

Eye-variant B

SM A 28737	345	556	567	666	656	655	543	—	109	7
SM A 28741	345	677	778	787	777	676	654	32	136	8

Acaste downingiae macrops (Salter)

BU H 132	567	889	989	989	999	887	654	3	163	9
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Acastoides constricta (Salter)

SM A 28719	456	666	676	666	565	543	—	—	98	7
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variant A lie in a curve just inside the facial suture. Visual surface very compact, just over twice as wide as it is high. All the dorso-ventral files diverge ventrally at quite a high angle. Lenses (Tables 1, 2) arranged in a similar pattern to those of eye-variant A but very much more closely packed. The largest lenses are often contiguous, even in small specimens.

Character of visual field. As can be seen on the stereogram (text-fig. 6g, h), the longitudinal visual limits are normally 0–180°, in both eye variants. The latitudinal limits are somewhat variable, but are generally in the region of 10–20° in eye-variant A and 8–20° in eye-variant B. The upper visual limit is fully latitudinal (text-fig. 6g, h) except at the extreme anterior and posterior edges where it rises slightly higher. The lower limit

is latitudinal anteriorly, but towards the rear the elevation of the lowest lens-axes rises, so that a shallow postero-ventral 'lacuna' is formed. In some cases a smaller anterior lacuna may be present.

TABLE 2—Dimensions of cephalon, eyes and lenses (in mm.)

Acaste downingiae (Salter) s. str.*Eye-variant A*

Specimen	Cephalon		Eye					Lens diameters		
	*L(sag.)	W	L(max.)	L(min.)	W(max.)	W(min.)	H	Large	Average	Small
SM A 28744	3.5	7.5	1.9	1.55	1.2	0.9	1	0.1	0.1	—
SM A 28764	5.5	12	2.5	2.1	1.5	1.25	1.3	0.14	0.125	—
SM A 28749	7.5	14	2.9	2.5	2.2	1.5	2	0.175	0.165	—
SM A 28720	10.5	18	3.5	3.1	2.25	1.5	2	0.25	0.23	0.1
SM A 28743	11.5	21	4	3.6	2.4	1.75	2.25	0.275	0.25	0.175

Eye-variant B

SM A 28737	5	9	1.75	1.5	1.25	1	1	0.14	0.125	—
SM A 28741	8	15	3	2.75	2	1.75	1.75	0.175	0.165	0.05

Acaste downingiae macrops (Salter)

BU H 132	6.5	11	3.5	2.5	2.5	2.0	2.25	0.25	0.2	—
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Acastoides constricta (Salter)

SM A 28719	7	10	3	2.3	2	1.5	1.7	0.2	0.175	0.075
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* L, W, H = length, width, and height as in text-fig. 1.

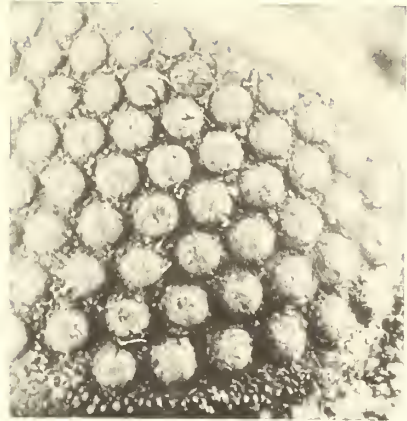
The strong differentiation between plan and profile curvature of the visual surface results in the concentration of the lens-axes into distinct and widely spaced 'visual strips', which of course correspond to the dorso-ventral files and diverge radially from the top to the bottom of the visual field. In the anterior and posterior visual strips of the larger specimens (text-fig. 5e, f) the lowest lens axes form a higher angle with the polar meridian than the upper ones. In the region of file 8 each strip tends to lie in a single longitude, but anteriorly and posteriorly they become more oblique and are often curved. The average spacing of adjacent strips is in the region of 7° at the top and 10° at the bottom, but posteriorly it may increase to 10° and 15° respectively.

EXPLANATION OF PLATE 2

Figs. 1–4. *Acaste downingiae* (Salter) s. str., eye-variant A. Wenlock Limestone. Silurian. Dudley, England. 1–3, SM A 28720, right eye. 1, Lateral aspect, $\times 7.5$. 2, Lenses near the anterior margin, $\times 25$. 3, Dorsal aspect, $\times 7.5$. 4, SM A 28743. Right eye, lateral aspect, $\times 7.5$.
Figs. 5–8. *Acaste downingiae* (Salter) s. str., eye-variant B. Same locality and horizon. 5, 6, SM A 28737. Left eye, lateral and dorsal aspects, $\times 20$. 7, 8, SM A 28741. Left eye, lateral and dorsal aspects, $\times 7.5$.



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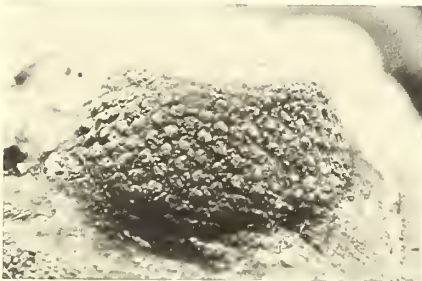
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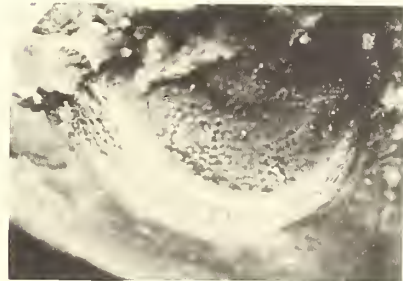
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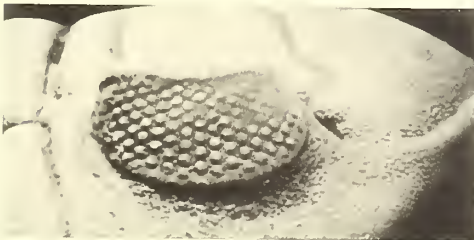
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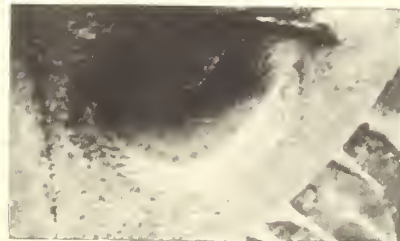
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Angles separating adjacent lens-axes within the strips are very low. Even in the youngest stages, they are only 1° or 2° in the long central files, and 3° or 4° in the outer files.

The visual field of both eye-variants is very similar, but in eye-variant B the visual strips are more regular and less highly slanted.

Post-larval development of the visual surface. Ontogenetic studies of the eyes are complicated by the existence of the two eye-variants. This has led to divergent interpretations of ontogeny. For example, Clarke (1889) charted the number and arrangement of the lenses in various specimens of *Phacops rana* (Green), and showed that there was a definite relationship between the number of lenses in the eye and the size of the specimen. Equating size with age he concluded that the number of lenses increased from youth to maturity, and then decreased from maturity to senility. He believed that the extra lenses present in the smaller specimens had been later absorbed by sclerosis, due to the growth of the interlensar sclera or the migration of the lenses below the surface of the palpebral lobe. The strong inflation of the sclera in the older specimens was used as evidence in support of this hypothesis.

Beckmann (1951), who worked with *Phacops* cf. *breviceps* and *Phacops schlotheimi*, found no such apparent diminution in lens number with senility, but only an increase until full maturity was reached. Further, using Clarke's measurements of specimens of *P. rana*, Beckmann produced a graph showing the number of lenses compared with the width of the cephalon. This graph indicated that Clarke's material was composed of two distinct elements, in one of which the cephalons were small and the lens number large, and in the other the cephalons were large and the lens number small. He suggested that since Clarke's material came from various localities in North America, two ecologically distinct faunas were present which had probably been mixed prior to examination. In the species which Beckmann investigated there was apparently only one fauna, and hence only one type of eye.

The probability that Clarke had inadvertently included more than one type of eye in his analyses is enhanced by Stumm's (1953) systematic revision of *P. rana*. Stumm distinguished a number of subspecies using the character of the eye as a diagnostic feature. The significance of Stumm's work is to be discussed in a later paper.

Neither Beckmann nor Clarke referred to the work of Barrande (1852, p. 514, pl. 21) who recorded the lens number and distribution in 12 specimens of *Phacops fecundus* Barrande, noting that the largest specimens never had as many lenses as the smaller ones. Barrande attributed this to the considerable degree of intraspecific variation characteristic of this species. His figures (pl. 21, fig. 19) show that the longest file of the largest specimen only has 5 lenses, whereas the maximum number recorded, in a smaller specimen, was 9. In the largest specimens the interlensar sclera is inflated and the lenses are rather widely spaced. Hence there is a strong resemblance between the condition of *P. rana* and that of *P. fecundus*.

The present studies tend to confirm Beckmann's view that two distinct elements were present in Clarke's material. But in *Acaste downingiae* s. str. the two variants commonly occur in faunas which were collected at a single locality and are, therefore, unlikely to be the result of ecological control. No evidence of lensar sclerosis or absorption by the palpebral lobe has been collected, and Clarke's hypothesis of decrease of lens number with senility has been abandoned.

In the earlier growth stages the distinction between the two eye variants is less marked. Immature specimens of eye-variant A may have small genal spines resembling those of eye-variant B, which become progressively reduced and finally disappear. Thus in the series referred to, A 28744 has a short genal spine, A 28764 has pointed genal angles, A 28749 has a barely perceptible point, and in A 28720 and A 28743 the genal angles are fully rounded, with no trace of a point.

During ontogeny the eyes in eye-variant A double in length and more than double in height in their development from the youngest preserved stage. The relative increase in height is due to an increase in number of lenses in the files. The angle at which adjacent files diverge decreases through development. The size and spacing of the lenses increase progressively from youth to maturity but remain approximately constant relative to the size of the whole visual surface.

The conclusions of Clarke and Beckmann, that the lenses increased in number with age, and in a particular order, have been confirmed in general, though it seems that the eye of *A. downingiae* is rather more variable than the species which they investigated.

From Table 1 and the diagrams of the visual surface (text-fig. 4) we may draw the following conclusions:

1. The full lens complement of the upper and accessory upper horizontal rows was already developed from an early stage (SM A 28744) and no more lenses were added to the upper ends of the dorso-ventral files; these rows remained complete and separate entities. Beckmann showed that in *P. cf. breviceps* and in *P. schlottheimi* some lenses were added at the upper ends of the files, but his youngest specimens seem to represent an earlier stage in development than any yet seen in *A. downingiae*, where the youngest specimen has already a maximum of seven lenses per file. It is possible that in earlier stages in the development of the eye of *A. downingiae* lenses may have been added immediately below the facial suture.

2. As Clarke has suggested, new lenses were added exclusively at the lower ends of the files, i.e. at the lowest points of the visual surface, at least during the growth stages studied. But as the species is more variable than those which Clarke and Beckmann studied, it has not been possible to produce diagrams like those of Beckmann (Abb. 278/3), showing the order of development of the lenses. The newly developed lenses are small and set closely below the preceding lenses. Generally they are circular but in the young stages of eye-variant A they are elliptical. The immature lenses may be compared with the corresponding lenses on larger specimens, and by comparison with the latter it appears that only when they have grown to their full size do new lenses arise below them. The manner of emplacement of new lenses appears to resemble that described by Clarke for *P. rana*. He showed by sections that the 'ommatidial cavities' arise by evagination of the sclera from below, and these cavities meet with the outer surface where

EXPLANATION OF PLATE 3

- Figs. 1-3. *Acaste downingiae* (Salter) s. str., eye-variant A. Wenlock Limestone. Silurian. Dudley, England. 1-3, SM A 28720. Lateral, dorsal, and anterior aspects of enrolled specimen, $\times 2$.
 Figs. 4-9. *Acaste downingiae macrops* (Salter). Same locality. BU H132, 4, 5, 6, 9. Lateral, anterior, and dorsal aspects of enrolled specimen, $\times 4$. 7, 8. Right and left eyes, lateral aspect, $\times 7.5$.
 Figs. 10-12. *Acastoides constricta* (Salter). Same locality. 10, SM A 28719. Right eye, lateral aspect. 11, 12, SM A 28719. Lateral and dorsal aspects of enrolled specimen, $\times 3\frac{1}{2}$.



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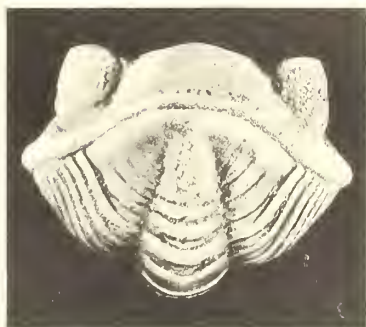
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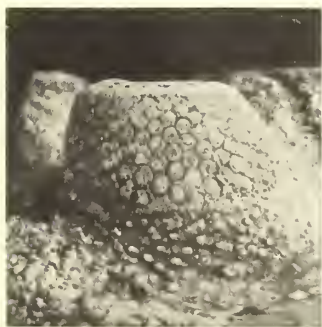
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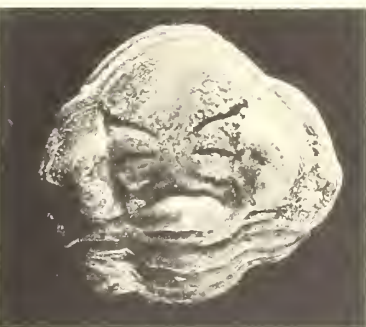
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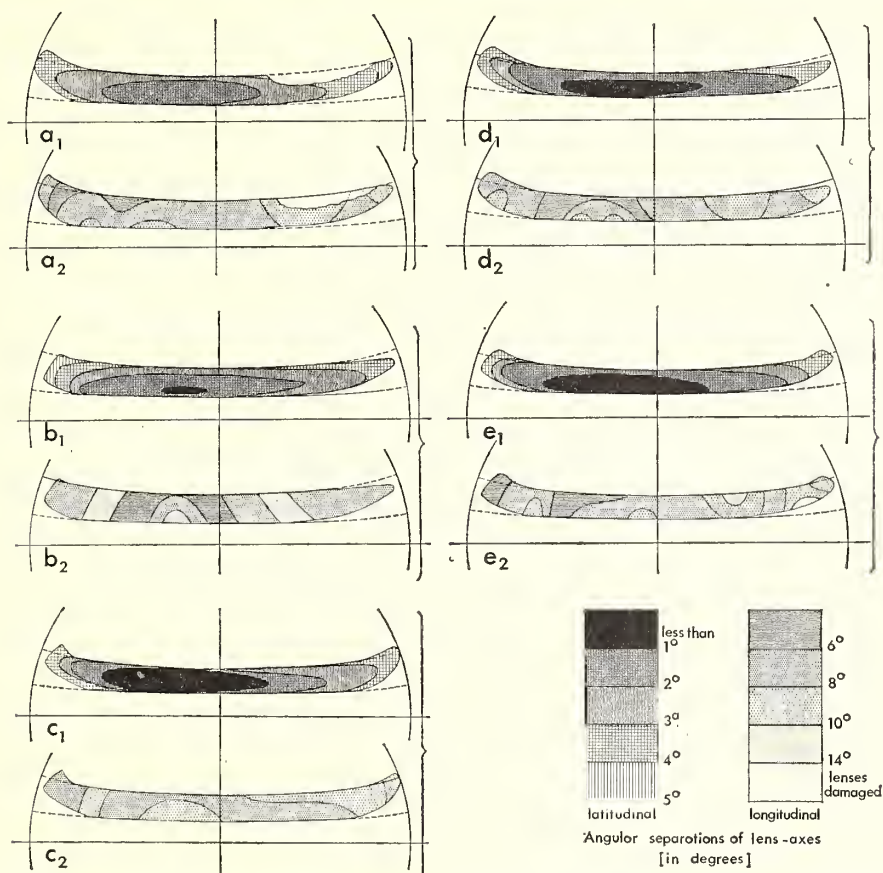


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there may be a corresponding inward invagination. Some of his sections showed immature cavities which had not penetrated the outer surface. The size of all the lenses increases progressively during ontogeny, remaining approximately constant relative to the size of the whole visual surface. There are marked variations, however, in the size of the lenses in different parts of the visual surface. The lenses along the upper border,

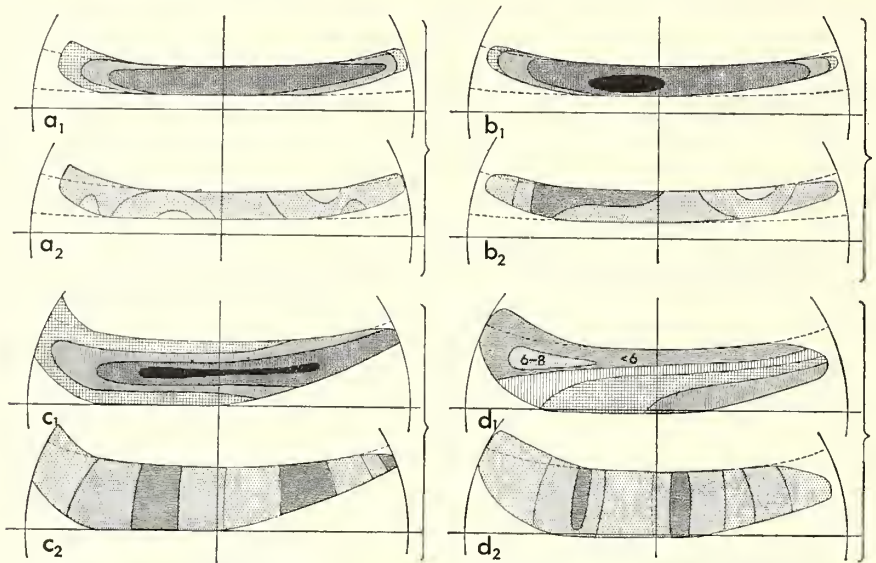


TEXT-FIG. 7. Latitudinal (a_1, b_1 , etc.) and longitudinal (a_2, b_2 , etc.) angular separations of the lens-axes, axial angles represented by contoured stereograms (cf. text-fig. 5). *a-e. Acaste downingiae* (Salter) s. str., eye-variant A. *a*, SM A 28744, left eye; *b*, SM A 28764, right eye; *c*, SM A 28749, left eye, *d*, SM A 28720, right eye; *e*, SM A 28743, left eye.

and to a lesser degree, the lower border remain relatively small, whereas those in the antero-lateral and postero-lateral sectors become relatively large. The differentiation is more pronounced in the later growth stages.

Changes within the visual field are represented by a series of stereograms (text-figs. 7, 8) which show the angular separations of the lens-axes by contouring. Latitudinal and longitudinal separations are indicated on separate diagrams. For latitudinal separations 1° contours were found to be suitable, but owing to the irregular spacing of the visual strips, 2° and 4° contours have been used to show longitudinal separations.

It is apparent from these and from the original stereograms (text-figs. 5, 6), that throughout the development of the eye, there are no major changes in the angular extent of the visual field. Apart from some slight intraspecific variation, the angular range of vision of an eye with 127 lenses differs little from one with 159. The longitudinal extent of vision of specimens with 22, 23, or 24 files is virtually the same (180°) and whether there is a maximum of 7, 8, or 9 lenses per file, the latitudinal extent is always of the order of 11° in eye-variant A, or 13° in eye-variant B. The extra lenses added with growth are orientated so that their axes remain within the prescribed visual



TEXT-FIG. 8. Latitudinal (a_1 , b_1 , etc.) and longitudinal (a_2 , b_2) angular separations of the lens-axes. Cf. text-fig. 6. *a*, *b*, *Acaste downingiae* (Salter) s. str., eye-variant B. *a*, SM A 28737, left eye; *b*, SM A 28741 right eye; *c*, *Acaste downingiae macrops* (Salter), BU H 132, composite figure from both eyes; *d*, *Acastoides constricta* (Salter), SM A 28719, right eye.

field. As the number of lenses increases, their latitudinal separation decreases, particularly (text-figs. 7 a_1 , b_1 , c_1 , etc., 8 a_1 , b_1 , c_1), in an elliptical region in the lower central part of the visual field surveyed by the longest files ($40\text{--}120^\circ$ long.; $10\text{--}17^\circ$ lat.). At all stages during ontogeny zones of increasing latitudinal separation are concentric with this region and the highest separations are found at the anterior and posterior visual limits. The profile curvature of the visual surface remains virtually constant throughout growth. The latitudinal elevation of the lowermost lens-axes must rise as new lenses are added below them, hence the axial bearing of any one of these new lenses will be similar to the original direction of the lens-axis now above it.

Changes in the longitudinal separation of the visual strips are less apparent, chiefly because so few lenses are added at the anterior and posterior edges of the eye. The total number of visual strips increases only from 22 to 24, and the pattern in which these strips are arranged remains constant throughout (text-figs. 5, 6). The appearance of the visual strips reflects the topographical situation of the lenses on the visual surface.

When the eye of *A. downingiae* s. str. is examined from directly above (text-fig. 1b), each lens of the anterior files appears slightly offset on the curving visual surface with regard to the lenses below and above it so that the axes of the lower lenses are directed more anteriorly than those of the upper lenses of the same file. This angular difference decreases posteriorly so that in the longest files all the lenses in one file have about the same longitudinal axial bearing. In the succeeding files the reverse situation to that of the anterior files is apparent.

Thus on the stereograms (text-figs. 5, 6) the separation of the visual strips corresponding to these files increases vertically except for the central longitudinal strips, which correspond to files 8 and 9. In young specimens the visual strips are almost straight. In older specimens the new lenses which have been added to the lower ends of the diagonal rows each have a slightly different longitudinal axial bearing from the lenses about them (except in the longitudinal strips), so that the total longitudinal range of the diagonal visual strips increases with age. On the stereogram the strips now become more highly slanted and may be curved. The tendency for the axis of the top lens of any one strip to have the same longitudinal bearing as that of the bottom lens of the adjacent strips, in the anterior and posterior parts of the visual field, appears in the youngest stages and becomes more pronounced during the later development of the eye. This is apparently a device which enables the whole of the visual field to be covered by the visual strips with maximum economy of lenses. The apparent complexity of the contoured stereograms showing longitudinal separations of the lens-axes (text-figs. 7 a_2 , b_2 , c_2 , etc.; 8 a_2 , b_2) is the result of the variability in spacing of the visual strips, which may range from 5° to 12° or more.

Comparison of the two sets of contoured stereograms (text-figs. 7 a_1 , a_2 , b_1 , b_2 , etc., 8 a_1 , a_2 , b_1 , b_2) indicates that regions of maximum or minimum longitudinal separation do not necessarily coincide with like regions of latitudinal separation.

At this point it is interesting to consider the coverage of the visual field by lenses of varying sizes. This is again best represented by contoured stereograms (text-fig. 9). These stereograms indicate how, whilst the lenses increase in size during ontogeny, those regions of the visual field covered by the largest and by the smallest lenses remain relatively constant. The actual pattern of coverage differs in the two eye-variants. Thus in eye-variant A, the largest lenses survey regions close to the anterior and posterior visual limits, of which the anterior has the wider extent; whereas in eye-variant B, the lenses are more uniform in size and the two regions are less well marked.

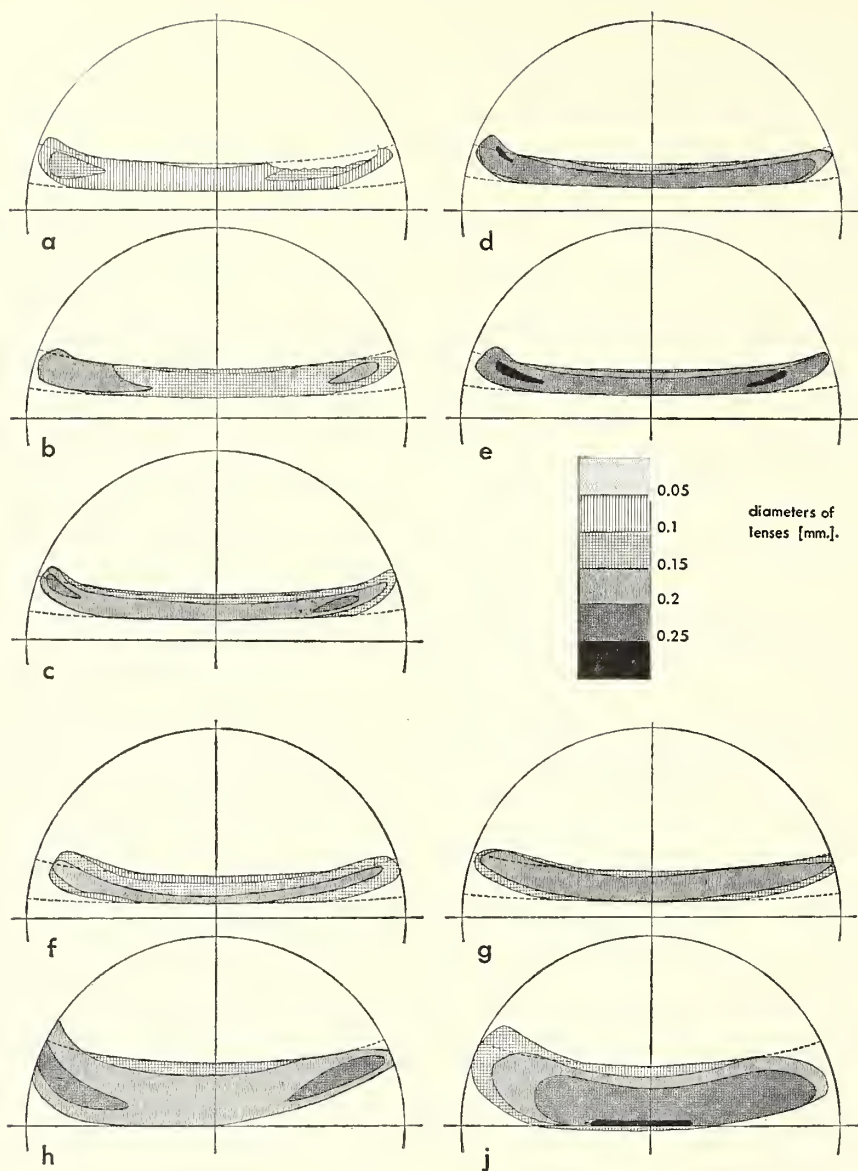
Finally, the above stereograms (text-fig. 9), may be compared with the paired stereograms showing axial separations (text-figs. 7, 8). There is some degree of relationship in this species between the size of the lenses and their latitudinal axial separations. The largest lenses cover the regions where axial separations are high, i.e. at the extremities of the visual field. The relationship between lens sizes and longitudinal axial separations is somewhat less obvious owing to the greater variability of the latter.

Acaste downingiae macrops (Salter 1864)

Plate 3, figs. 4–9.

1864 *Phacops* (*Acaste*) *downingiae* Murchison var. β *macrops* Salter, pp. 26–27, pl. 2, figs. 26–29.

Salter's (1853) description of *A. downingiae* included a brief account and figure of the



TEXT-FIG. 9. Contoured stereograms showing coverage of different regions of the visual fields by lenses of various sizes. *a-e*, *Acaste downingiae* (Salter) s. str., eye-variant A. *a*, SM A 28744, left eye; *b*, SM A 28764, right eye; *c*, SM A 28749, left eye; *d*, SM A 28720, right eye; *e*, SM A 28743, left eye; *f, g*, *Acaste downingiae* (Salter) s. str., eye-variant B. *f*, SM A 28737, left eye; *g*, SM A 28741, right eye; *h*, *Acaste downingiae macrops* (Salter), BU H 132, composite figure from both eyes; *j*, *Acastoides constricta* (Salter), SM A 28719, right eye.

'large-eyed' form of the species, in which he noted that the visual surface was almost double the size of the normal type and possessed about 180 lenses. In 1864 he gave this varietal status.

A single small enrolled specimen, BU H 132 from the Wenlock Limestone of Dudley has been analysed. Both eyes are preserved undistorted but in each the visual surface is slightly damaged and some lenses are missing. The surface of the left eye is the more complete but a few of the posterior lenses have been destroyed. The posterior region of the right eye is entire but anteriorly patches of lenses are absent. The diagram (text-fig. 4j) representing the projected visual surface is composite and is derived from measurements of the existing parts of both eyes.

Morphology of eyes. Eye very large, prominent, set towards the rear of the cephalon, and extending from glabellar furrow 3p to the posterior marginal furrow. Both the anterior and posterior edges of the eye lie almost in the same exsagittal plane. In profile the base of the eye is situated rather low on the cephalon, at less than half the distance from the genal angle to the crown of the glabella, and the palpebral lobe stands at about the same level as the latter. In plan the visual surface is parabolic and sharply flexed about the transverse line; profile curvature moderate, strongest nearest the upper and lower borders. The visual surface rises sharply from the indistinct eye platform, is bounded ventrally by a shallow groove, and projects laterally near to the antero-lateral border of the cephalon. Both eye borders are parallel. Palpebral lobe moderately broad (tr), flat and smooth, declining very sharply adaxially to the sunken palpebral furrow, which at its point of maximum flexure in the transverse line turns sharply through 90°. Palpebral area smooth, shelving gently toward axial furrow and open posteriorly.

Lenses (see Table 1) disposed regularly in 22 dorso-ventral files.

All files diverge ventrally at a very low angle. Lenses quite closely packed, showing comparatively little variation in size (see Table 2), though in the central files the largest lenses are slightly smaller than those of the penultimate anterior and posterior files. The first and last files have small lenses and the lowest lenses of the diagonal rows are of about the same diameter. Very small lenses are present in the centre of the upper horizontal row. An accessory upper horizontal row is present, which extends from files 13 to 17.

Interlensar sclera planar and finely granular. A hexagon of larger granules surrounds each lens.

Character of visual field. The stereogram (text-fig. 6j) shows the visual field, which has longitudinal visual limits of about 0–180°, with a small anterior overlap, and a maximum longitudinal range of 0–28°. The upper visual limit is fully latitudinal, whereas the lower is equatorial only between files 1 and 12, and rises posteriorly so that there is a fairly deep postero-ventral lacuna with a maximum latitudinal extent of 0–18°.

The lens-axes form distinct visual strips, which contrast with those of *A. downingiae* s. str. in several respects, most notably in that all except the few posterior strips are longitudinal. As a result of the parabolic plan curvature of the visual surface, these strips tend to be clustered in two regions, in front of and behind the polar meridian, where they are normally separated by angles of less than 10° longitude (text-figs. 6j, 8c₂). Between the more widely spaced central strips the separation may be as high as 15°.

Differentiation in the profile curvature of the visual surface leads to strong variation

in latitudinal separation of the lens-axes within each strip (text-figs. 6j, 8c₁). In a longitudinal band lying between 8° and 20° lat. axial angles are low (2–3°), but above and below this band the separation of lens-axes increased quite regularly to 6° or more.

The regions of minimal latitudinal and longitudinal separation almost coincide in *A. downingiae macrops*. The composite text-fig. 9h shows the coverage of the visual field by lenses of both eyes. Although the latitudinal extent of vision is greater than in *A. downingiae* s. str. a remarkably similar pattern is apparent. Likewise the sizes of the lenses bear no relationship to their axial separations.

Acastoides constricta (Salter 1864)

Plate 3, figs. 10–12.

1864 *Phacops (Acaste) downingiae* Murchison, variety or subspecies ϵ *constrictus* Salter, pp. 27–28, pl. 2, figs. 13–16.

1954 *Acaste (Acastoides) constricta* (Salter 1864); R. and E. Richter, pp. 17–18, pl. 3, figs. 42, 43.

Salter (1864) noted that the eyes of this species were small and set very close to the glabella, having a total of 130 lenses each.

A single small enrolled specimen (SM A 28719) from the Wenlock Limestone (Silurian) of Dudley, was analysed. The right eye is complete and perfectly preserved. The left is damaged.

Morphology of eyes. Eyes small, not very prominent, lying close to glabella, situated in the posterior part of the cephalon, and extending from between glabellar furrows (1p) and (2p) to the posterior marginal furrow. Both the anterior and posterior edges lie in the same exsagittal plane, the anterior being separated from the glabella by a narrow space. In profile the base of the eye is set high upon the cephalon, almost two-thirds of the distance between the genal angle and the crown of the glabella, and the palpebral lobe is level with the latter. Plan curvature moderate, increasing behind the transverse line, profile curvature about half the former, decreasing posteriorly. The visual surface rises sharply from librigena, is bounded ventrally by a very shallow groove, and does not project laterally as far as the antero-lateral cephalic border. Both eye-borders are parallel. Palpebral lobe moderately broad (tr), inflated and somewhat tuberculate, bounded adaxially by a row of shallow pits, and shelving first gradually, and then steeply to the indistinct palpebral furrow. Palpebral area small, almost flat, and open posteriorly.

Lenses (text-fig. 4k and Table 1), disposed regularly in 18 dorso-ventral files. All files diverge ventrally at a rather low angle. Lenses packed so closely that over most of the visual surface they are hexagonal and only the smallest lenses are rounded. Within each file they increase ventrally in diameter, though in the first and last two files their diameter is constant. An accessory upper horizontal row of small round lenses extends from files 8 to 16. The lenses of the anterior two or three files are small.

Interlensar sclera hardly discernible between the hexagonal lenses, but where visible below the facial suture it is planar and smooth.

Character of visual field. The maximum extent of the visual field (text-fig. 6k) is 6–174° long.; 0–27° lat. The upper visual limit anteriorly lies slightly above the 27° latitude and the lower is truncated by a small anterior and a larger shallow posterior lacuna.

The lens-axes are widely separated and form longitudinal visual strips which are relatively indistinct because throughout the visual field longitudinal separations are rarely more than twice the latitudinal. The variation in longitudinal axial angles (text-figs. 6*k*, 8*d*₂) resembles that observed in *A. downingiae macrops* so that there are two regions of minimal separation, anterior and posterior to the polar meridian. The latitudinal axial angles, however, vary in a manner quite unlike those hitherto observed (text-figs. 6*k*, 8*d*₁). The region of minimal latitudinal separation lies directly above the postero-ventral lacuna, and the axial angles increase regularly to the upper and anterior regions.

The largest lenses (text-fig. 9*j*), unlike those of *A. downingiae* cover the lowermost central part of the visual field, but this region of coverage does not really correspond with the areas of maximal or minimal axial separation. Whereas the structure and visual characters of the eyes of *A. constricta* differ radically from those of *A. downingiae*, similar features have been observed in *Dahmannites caudatus* (Brünnich) and in other Phacopina.

COMPARATIVE VISUAL PHYSIOLOGY

A fuller interpretation of the physiology of vision in these trilobites will be deferred until descriptions of the visual attributes of other schizochroal eyes have been published, but the nature of vision in the trilobites studied here is briefly considered with reference to that of recent arthropods.

Visual powers of single ommatidia. The fundamental units of which all modern compound eyes are constructed are the radially arranged ommatidia. Each of these has the form of a tapering cylinder whose upper end is capped by a lens capable of transmitting light to the photoreceptive retinular cells below. In the eyes of trilobites only the lenses and the interlensar sclera are ever preserved and the structure of the eye below this level is unknown. It must be assumed that the underlying regions were similar in their organization to those of recent arthropods, and that below each lens lay an ommatidium-like unit.

Considering the remarkable variability in the separation of the lens-axes and presumably therefore of the ommatidia, it is of some importance from the physiological viewpoint to know the angular receptivity to light of single ommatidia, and whether or not the visual fields of adjacent photoreceptors could have overlapped. The possible conditions in trilobites cannot be ascertained directly, but may be inferred from the comparable eyes of recent arthropods, though even in these the functions of single ommatidia as individual units is hardly known.

Burt and Catton (1954) working with *Locusta*, and Waterman (1954) with *Limulus*, have shown that single ommatidia have a wide range of directional sensitivity. In *Locusta* each ommatidium has a visual field of about 20° solid angle, and in *Limulus* it has been shown that whereas high light sensitivity is centred within 10–20° of the optic axis, responses were still given to reasonable light intensities up to 80° or 90° away from it.

In such eyes the visual fields of adjacent photoreceptors must overlap considerably. It is possible that in trilobites the cones of light-receptivity of neighbouring ommatidia were wide enough to extend laterally into the spaces between their axes and even between

the visual strips at a short distance from the visual surface, and hence there may have been no gaps in the object space. As in *Limulus*, however, high sensitivity was probably limited to the region of the optic axis.

Types of perception in compound eyes. Von Buddenbrock (1935) classified compound eyes in a scale of progressive efficiency as being capable of (1) light and dark perception, (2) direction perception, (3) movement perception, and (4) form perception. Only the more advanced compound eyes are capable of the last, which as recently shown (Burt and Catton 1962; Rogers 1962) seem to operate by the production of successive diffraction images, which can only work efficiently in an eye consisting of large numbers of small lenses. In these eyes, visual acuity may be three or four times as high as the angular separation of the lens-axes would indicate. The schizochroal eyes of trilobites with their small number of large lenses, are of a lower grade of organization than those of many insects. It is unlikely that their large lenses could form diffraction images and the strong degree of astigmatism of the eyes of *Acaste* which would naturally result from the extreme differentiation in lens-axis separations in different directions would tend to preclude form perception.

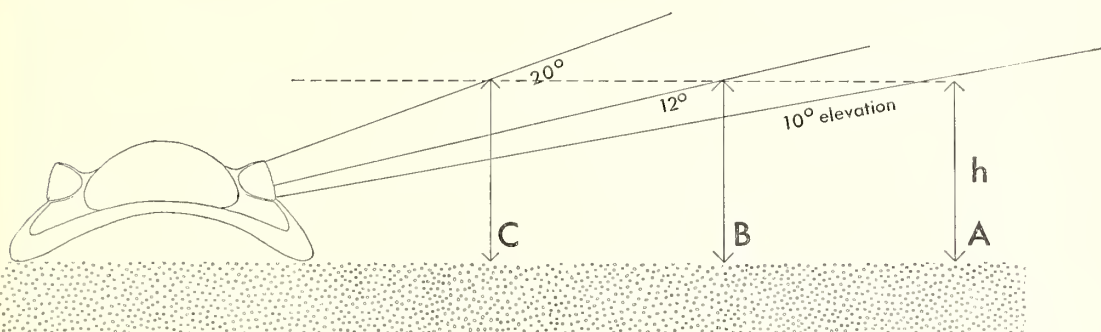
Movement perception in Acastinae. The astigmatism, which in Acastinae must amongst other factors have limited the possibility of image formation, nevertheless seems to have been an intrinsic part of their visual organization, and could indicate that the eyes may have been adapted for the perception of movement. Astigmatic eyes are known in other arthropods. Amongst insects, strong differentiation in the surface curvature of the eye and in the separation of the ommatidia resulting in a considerable degree of astigmatism was noted by Exner (1891). It has been described in sections of the eye of the honey bee (Baumgärtner 1928) and of many other insects (del Portillo 1936). Some experimental evidence (Hecht and Wolf 1929) indicates that in the bee visual acuity in different planes varies with the degree of ommatidial separation. In these insects, however, the angular separation of adjacent ommatidia in the horizontal axis, even at its maximum, is never more than three times that in the vertical axis.

In *Acaste*, however, the equivalent angular separation of lens-axes may be up to fifteen times greater in the horizontal than in the vertical plane. The visual strips thus formed are established from a very early stage in ontogeny. Those visual strips, which are distributed radially in such a manner as to cover the whole of the visual field leaving no part of its total longitudinal extent unsurveyed by at least one lens-axis, are the most striking and apparently the most important characteristic of vision in *Acaste*. Their existence, however, necessitates the constriction of the overall angular range of vision to an extremely narrow visual field which in *A. downingiae* s. str. may be of only 10° latitude, and thus imposes a limit upon the efficiency of the eye as a whole. The visual fields of *A. downingiae macrops* and *A. constricta* are twice as wide. In the former, well-developed strips occur in a central longitudinal belt, but in the flanking belts of this eye, and in the whole visual field of *A. constricta* visual strips are indistinct, and the ratio of axial separation in horizontal and vertical planes is only 2:1, like that of many insects.

The visual fields of both *A. downingiae macrops* and *A. constricta* are truncated ventrally, both anteriorly and posteriorly, by quite deep lacunae, in contrast with the shallow posterior lacuna of *A. downingiae* s. str. All such posterior lacunae may be

interpreted as an adaptation which prevents vision in the posterior and ventral region being obscured by the high posterior border of the cephalon.

The eye of *Acaste downingiae* s. str. could have detected movement by means of the visual strips. Burt and Catton (1962) have stated that 'for perception of movement of a discontinuous object there must be discontinuities in the image formed in the eye at photoreceptor level'. Such discontinuities would be provided by the visual strips. For, if, as has been already suggested, the highest sensitivity to light of the ommatidia was



TEXT-FIG. 10. *Acaste downingiae* (Salter) s. str., eye-variant A. Anterior view of cephalon showing latitudinal limits of vision of 10° and 20° . An object of height h approaching the trilobite would not be detected at A. At B it would come within the lower part of the visual field, and at C it would be sighted by the uppermost lenses.

centred in the vicinity of the optic axis, then uniform light intensity surrounding the trilobite would be registered by the trilobite's eye as a series of lighter and darker bands relating respectively to the regions covered by and in between the visual strips. Any dark object moving horizontally within the visual field would pass across successive bands (strips) and temporarily occlude them. A conception of the size, speed, and direction of the moving object would be given by the changing pattern. Dr. Rudwick has suggested how such an eye might also be able to detect the movement of an object towards the trilobite. It has been shown that the lower limit of the visual field of *A. downingiae* s. str. is directed at a few degrees above the equator (text-fig. 10). A distant object at A would lie below the visual limit or on its periphery. The same object at B would lie within the lower part of the visual field, and hence would be detected by the lower lenses. If the object approached to C, it would come within the visual compass of the upper lenses. Hence the horizontal approach of a predator along the sea floor would be recorded by the eye as the progressive darkening of the visual strips from the bottom to the top. To what extent the mutual overlap of the cones of vision of the individual ommatidia would affect the eye's efficiency for movement perception is uncertain.

It is also worth noting that the highest concentration of lens-axes per strip is found in that region of the visual field immediately anterior to the polar meridian, and this is apparently the area of maximum sensitivity. A comparable condition is known in the eye of the honey bee (Baumgärtner 1928).

It is clear that if each photoreceptor had a high angular range of light sensitivity, the apparent visual field as recorded upon the stereograms must have been surrounded by a peripheral zone or penumbra, from which visual impressions may have still been

received even if these were less direct. The outer zones of the visual field of *A. downingiae macrops*, which are surveyed by fewer lens-axes than the central horizontal band, presumably received less distinct visual impressions than the latter but they have the effect of extending the overall visual field down to the equator and latitudinally upwards. Within these zones vision appears to have been adapted less for the perception of movement than for the perception of varying light intensity. These flanking zones which are surveyed by relatively large lenses, cover those regions which in the eye of *A. downingiae* s. str. would be blind or penumbral. In *A. constricta* the visual strips are indistinct and were less efficiently adapted for movement perception than those of *A. downingiae* but this is offset by the advantage of the extended visual field.

The differentiation in lens-size within the visual surface must affect the physiology of the eye as a whole. The large lenses gathered most light but the small lenses of the upper central region inevitably transmitted less bright illumination to the photoreceptive cells below them. Thus the visual strips do not have uniform illumination along their whole length, and as is shown in text-fig. 7, those strips in which the lens-axes have the lowest angular separations are not necessarily those covered by the largest lenses. In *A. downingiae* s. str. there is, as previously stated, a certain degree of relationship between the sizes of the lenses in individual eyes and the latitudinal separations of their axes. The axial separations of the largest lenses, which cover the extremities of the visual field, are high. This might perhaps be interpreted as an adaptation which would tend to even the illumination received by all the visual units of the eye, which would otherwise be unequal because of the lens-size differentiation throughout the visual surface. In *A. downingiae macrops*, and *A. constricta*, however, the areas of the visual field covered by the largest lenses show little correspondence with the regions covered by the greatest or least number of lens-axes.

Differentiation of lens sizes within the eyes is a feature common to all Phacopina, and normally follows a similar pattern to that of *Acaste*. *Acastoides* is exceptional. It may be concluded that throughout the evolution of Phacopina, varying degrees of differential curvature resulting in different types of vision were superimposed upon visual surfaces whose pattern of lens-size differentiation was already genetically fixed. This variation in lens-size apparently imposes a limitation upon the efficiency of vision, but may have originally been necessitated by the form of the ancestral eye. The eyes of *A. downingiae* s. str. may be adapted to function with more uniform sensitivity over the whole visual field in spite of the lens-size differentiation.

Ecological significance of vision in Acastinae. All the specimens studied were collected last century from the Silurian Wenlock Limestone of Dudley. The sedimentary features of this limestone have been described by Butler (1939, p. 56). Relatively shallow water conditions prevailed throughout deposition and the environment was principally that of a coral reef, with strong light and almost silt-free water, though at intervals the depth of water increased and corals were unable to grow. The exact horizons of the fossils studied and their locations are, however, unrecorded and it is unknown whether *A. constricta* and *A. downingiae macrops* are ever found in the same beds as *A. downingiae* s. str. The chief visual characteristics of *A. downingiae* s. str., i.e. the visual strips and small lenses, suggest that the eyes were primarily adapted for the perception of moving organisms in strong light, as would be expected in a shallow water environment.

Whether any inference of a deeper water or otherwise different environment may be drawn from the eyes of *A. downingiae macrops* and *A. constricta* is uncertain and further purely ecological work is required before any more definite statements can be made.

The two distinct eye-variants in *Acaste downingiae* s. str. may be tentatively interpreted as a feature indicative of sexual dimorphism. It has been suggested by previous authors that sexual dimorphism is exhibited in certain trilobites and is generally apparent as minor differences in the overall structure of the exoskeleton. More evidence relating to eye morphology comes from a study of other Phacopina, but analogy may be made with recent insects and crustaceans, where sexual dimorphism commonly affects the size and shape of the eye.

Lastly, it may be stated that the results obtained here give a strong indication of the normal life orientation of the phacopid cephalon. The visual fields of Phacopina and of *Acaste* in particular are usually in the form of long narrow bands which in life were undoubtedly orientated so that the trilobite had 360° vision in a horizontal plane.

When the cephalon is orientated so that the 'horizontal' lens-rows are actually aligned horizontally, then the visual limits are normally latitudinal. If this cephalon is examined from the side, the antero-lateral border (Pl. 3, figs. 3, 8, 9, 12) appears inclined, and the rear margin of the occipital ring forms a hood-like projection which would cover the articulating half-ring of the first thoracic segment.

On turning the cephalon towards the observer, the border forms an 'anterior arch' (Pl. 3, figs. 1, 6). This anterior arch is a constant feature of Phacopina and of many other groups of trilobites also. In Cheirurina it is often made very evident by the presence of hypostomes projecting below the antero-lateral border.

It is of interest to note the contrast between the cephalic attitude inferred here and that which Whittington (1956) deduced as the normal profile orientation of cephalae of Odontopleuridae. In this specialized group he noted that the cephalae seem to have been adapted for resting upon a flat surface on the tips of almost vertical spines produced from a horizontal antero-lateral border, or upon lateral extensions of the border itself. A cephalon in this orientation is tilted forwards through about 30°, relative to the attitude envisaged for phacopids, and it seems that the phacopid attitude is indicative of a different mode of life. Whittard (1939), Warburg (1939), and Whittington and Evitt (1954) have in turn touched upon the problem of the natural orientation of the cephalon but further studies are still required. When this has been determined it will be possible to deduce the manner of articulation of the thorax and pygidium relative to the cephalon. From these observations the life attitudes and certain environmental adaptations of such trilobites may possibly be inferred.

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MARINE BENTHOS, SUBSTRATE AND PALAEOECOLOGY

by G. Y. CRAIG and N. S. JONES

ABSTRACT. The distribution of marine benthos in the Irish Sea is influenced by the nature of the substrate. The majority of epifaunal species are suspension feeders or carnivores and are associated with rocks or coarse-grained sediments. The majority of infaunal species are deposit feeders and are associated with fine-grained sediments. The relationships of the organic content of the sediment and the physical nature of the substrate to the benthos are discussed. It is argued that epifauna, and benthos living in well-sorted sands, are more likely to be transported after death than most infauna. Fossil epifauna are most likely to be found *in situ* at unconformities, disconformities, and bioherms. Over half of the species of epifauna but only one-third of the species of infauna have hard parts and are preservable as fossils.

GEOLOGISTS are accustomed to the association of a rock facies and its contained fauna, and such terms as black-shale facies, sandy facies, and reef facies usually evoke a picture of well-known depositional environments and their faunas, relatable to the experience of the individual concerned. Yet in spite of the geologist's dependence on, and indeed intimate knowledge of sediments, he rarely pursues so far as he might the relationship between sediment and fauna. We believe that a discussion of certain aspects of the relationships between living organisms and their sediments may provide a useful contribution to a subject which is perhaps more appreciated by ecologists than by palaeoecologists. (A recent article by Purdie (1964) which appeared after this paper was submitted shows that geological appreciation of this problem is indeed growing.)

An important aspect of the relationship between marine faunas and sediments was demonstrated by Petersen (1913), who divided the benthos of the Danish seas into epifaunas and infaunas. He recognized as epifauna those animals living upon, or associated with extraneous matter or vegetation resting on, the substratum forming the bottom, and as infauna, animals living in the sediments forming the level sea bottom. Various other terms, such as epibionts and endobionts (Schafer 1956) have been introduced to overcome etymological objections and to include plants as well as animals. Epibenthos and endobenthos are perhaps more satisfactory, but the original terms are entrenched in the literature and will be used here. The epifauna may be divided into sessile forms, occurring on rock, shells, weeds, and other objects on the sea floor but rarely on sediments, and active forms which can move freely over the substratum (Buchanan 1958).

Influence of sediment on benthos. Grain size, the most obvious feature of a sediment, affects the organism both directly and indirectly. Feeding methods are related to grain size; mode of attachment or movement depends on plasticity or the availability of hard surfaces; organic content and grain size are frequently a reflection of the strength of bottom currents; and the aerobic or anaerobic nature of the sediment is generally a function of grain size, although it is basically dependent on the rate of water circulation.

Grain size and feeding methods. The distribution of the faunas of the central part of the northern Irish Sea is well known (Jones 1940, 1951, 1952, 1956). From published and

unpublished data it is possible to calculate the numbers of species of invertebrates on the various grounds off Port Erin, Isle of Man, in relation to the method of feeding. For this purpose they can most conveniently be classified as:

1. Suspension feeders (sestonophages)
2. Deposit feeders (detritus collectors and soil swallowers)
3. Carnivores
4. Uncertain feeding habit

There is no sharp distinction between epifauna and infauna, apart from ecological position, but infaunas are made up largely of species dependent for their food on detritus or plankton; that is, they are deposit or suspension feeders, together with a proportion of carnivores. Epifaunas, on the other hand, contain few or no deposit feeders but usually a number of specialized feeders such as browsers and sponge eaters (Thorson 1957), although these can in a broad sense be classed respectively as deposit feeders and carnivores. Epifaunal animals are naturally not adapted to burrowing as are many members of the infauna. They tend to be better protected than infaunal animals, with thicker shells, tests or carapaces.

Table 1 is an analysis of the feeding methods of 79 of the more abundant species of infauna. For each feeding method the species are classified by the grade of sediment

TABLE 1

<i>Feeding method</i>	<i>% on each type of deposit</i>				
	<i>Mud</i>	<i>Muddy sand</i>	<i>Fine sand</i>	<i>Gravel/Shell</i>	<i>Widely distributed</i>
Suspension	0	20.5	36.5	29	8.5
Deposit	62.5	61.5	54.5	33.5	58.5
Carnivores	37.5	9	9	29	16.5
Uncertain	0	9	0	8.5	16.5
Total number of species	8	24	11	24	12

to which they are confined or centred upon. Where they occur more or less equally on two or more kinds of sediment they are classified as 'widely distributed'.

In Table 2 the feeding habits of 56 species of epifauna are analysed.

TABLE 2

<i>Feeding method</i>	<i>% on each type of deposit</i>				
	<i>Mud</i>	<i>Muddy sand</i>	<i>Fine sand</i>	<i>Gravel/Shell</i>	<i>Widely distributed</i>
Suspension	0	0	0	31.4	33.3
Deposit	0	20	33.4	17.2	16.7
Carnivores	100	80	66.6	45.7	50
Uncertain	0	0	0	5.7	0
Total number of species	1	5	3	35	12

In Table 3 all species (368 in number) found on each ground during 1947 (including epifauna and infauna) have been analysed. No distinction is made in this case between species confined to one ground and those occurring on several. Where definite information is lacking a species is referred to its most probable feeding method.

TABLE 3

<i>Feeding method</i>	% on each type of deposit			
	<i>Mud</i>	<i>Muddy sand</i>	<i>Fine sand</i>	<i>Gravel/Shell</i>
Suspension	0	17.5	12.5	24.5
Deposit	56.5	52	54.5	26
Carnivores	43.5	30.5	33	49.5
Total number of species	23	127	68	150

There is a marked increase in the proportion of suspension feeders with the increase in grain size, from mud (where none was found) to gravel/shell deposits. Deposit feeders, on the other hand, show a proportionate decrease from the mud and sand environments to the coarser sediments. Carnivores depend on the presence of other organisms and may not be especially affected by grain size.

The grain size of the sediment therefore exhibits considerable control over the type of feeding mechanism acceptable in the different environments and provides an indication of the kinds of mechanism that may have been characteristic of past environments. The relationship is well known (see, for example, Sanders 1956).

Biomass and organic content. Biomass is low in fine-grained muds and well-sorted sands, and reaches maxima in muddy sand and shelly gravel deposits. Fine-grained sand, because of its susceptibility to erosion (see Hjulstrom 1935, Inman 1949) and its low organic content, is a relatively unsuitable medium for the support of benthos. But with an increase in organic content (and with it almost certainly an increase in the amount of mud) sand becomes an organically rich medium, ideal for benthonic life. The resistance of the sediment to erosion is increased, moreover, as the organic material and mud bind the sand grains together.

Zenkevitch (1963, pp. 89, 90) stated that as a rule in the Barents Sea the larger the amount of the fine-grained fraction of the sediment, the richer its organic content. In other words, in regions with favourable conditions for deposition of the fine-grained fractions, large amounts of detritus are also deposited, but, on the other hand, these regions are usually unfavourable for the development of bottom life, presumably because of a low oxygen content in the deposit. However, many regions with a sandy bottom and a rich fauna may have a low content of organic matter. Good vertical and horizontal circulation prevent the accumulation of organic matter on the bottom. Hence though one may accept the rule that seas rich in life have more organic matter in their sediment, in some a reverse relationship between the amount of bottom life and organic matter in the sea bed may be created.

Zenkevitch (p. 138) also quoted Idelson (1930) on the quantitative distribution of the fauna on the Spitzbergen bank. On the middle part of the bank, where the bed is

washed clean, the fauna is very scarce. At the edges of the shallow, however, the biomass increases sharply, some 95–99 per cent. of it epifauna. Further on at the slope of the bank the benthos biomass is again reduced and then, on the mud beds surrounding the bank, it rises again. The main factor conditioning this biomass range is the distribution of foodstuffs, mainly organic detritus. The high biomass at the edges of the shallow, consisting mostly of epifauna, is conditioned by the presence of rich detritus washed out from the central parts of the bank and brought by water as a solid suspension. Further on, the reduction of the biomass is due to conditions unfavourable for the development of epifauna and infauna. (This is apparently due, though not stated, to an increase in suspended matter, causing reduction in epifauna, and a lower amount of organic matter in the sediment, which is less favourable to infauna.) The last increase in biomass is due to the infauna, which receives here, in a comparatively calm zone, an abundant amount of sedimentary detritus.

The richest fauna of the Barents Sea grows on sandy silts and silty sand floors. Epifaunal species are numerous on hard floors in the regions of strong currents. Areas rich in infauna are usually poor in epifauna and vice versa. On the one hand, this is explained by the properties of the sea floor since infauna cannot develop in rocky or cliff floors. On the other hand, in some areas the floor could have given refuge to infauna, but the abundant epifauna had taken all the food supplies; the bottom may contain large amounts of sponge spicules and owing to mechanical factors may become unfit for benthos habitation. This occurs on the Kildin bank, where finely cartilaginous and sufficiently silted floors give support to a rich epifauna and are almost devoid of infauna.

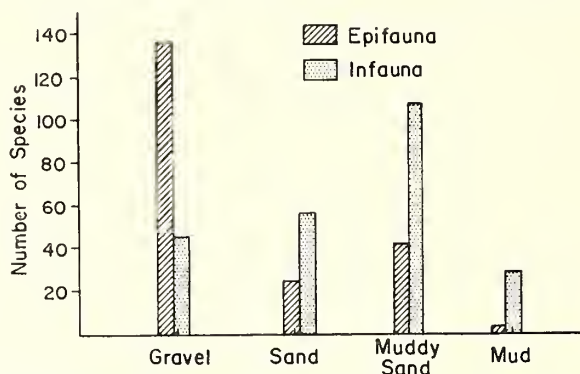
Savilov (1961) reported that in the northern Okhotsk Sea there is a replacement of one ecological zone by another in proportion to distance from the coast and increase in depth. In shallow coastal waters, rocks are occupied predominantly by a sessile epifauna consisting largely of suspension feeders. In the next zone on sandy bottoms mobile suspension feeders, mainly bivalves, predominate. This is followed by a wide zone of muddy sand with an infauna consisting mainly of detritus feeders, bivalves being replaced in the deeper parts by ophiuroids. Bottom feeders (soil swallowers) occupy the central deep part of the sea where there is a pronounced prevalence of sedimentation over erosion. Finally, in the depths from 1,000 to 3,000 m. the predominant group in the fauna is composed of immobile suspension feeders on soft bottoms. Carnivores cannot be allocated to any particular zone.

Nature of surface and plasticity of sediment. Firm surfaces, not necessarily rock outcrops, are suitable for attachment by such means as cementation, byssal or pedicle fixation, adhesion, etc. They also provide certain organisms, such as gastropods, with a suitable surface for locomotion. Many species are able to attach themselves to pebbles or shells exposed on the surface of an unconsolidated sediment.

Soft substrates vary considerably in their fluidity, which is a reflection of grain size and shape, and porosity (see Weller 1959). Relatively firm sediments may preclude the development of burrowers, as Chapman and Newell (1947) have shown with *Arenicola*; unstable sands do not encourage the development of life; and some muds are too soft to permit the survival of benthos. Indeed it is the common experience of geologists to find an absence of endemic life in originally fluid sediments, which have subsequently

revealed their instability by flowage (e.g. bottom structures in mudstones and slump structures in mudstones and sandstones).

Grain size and the distribution of epifauna and infauna. The varying abundance of epifauna and infauna in different sediments of the sea floor of the Irish Sea is shown in text-fig. 1. The proportion of epifaunal species decreases from gravel grounds to mud, whereas the proportion of infaunal species increases. A similar trend would be shown if the number of individual epifaunal and infaunal animals were plotted.



TEXT-FIG. 1. Histograms of the frequency distribution of infaunal and epifaunal species on different sediments in the Irish Sea off Port Erin, Isle of Man.

The factors which have determined these changing proportions are complex and interrelated. Three of them have been discussed—feeding methods, organic content, and physical nature of the sediment; all are related to grain size. A fourth, strength of bottom currents, is also relevant. Different species are influenced by these factors to differing degrees and it is not possible at this stage to categorize the species more closely than epifauna and infauna.

The rock terms used in text-fig. 1 suggest more mature deposits than are actually the case. The sediments are generally poorly sorted, including the two which yield the greatest number of species and individuals—muddy sand and shelly gravel.

Physically at least, the terms muddy sand and shelly gravel, as used in marine ecology, have much more in common than their names might at first imply. An organically rich muddy sand because of its suitability as a medium for benthonic life will, in the right conditions of temperature and salinity, support an abundant benthos. Under a low rate of sedimentation such an environment could develop into a shelly sediment in which the range of particle size (matrix+shells) could be as great as or even greater than that of a gravel/shell bank. The major difference between the two environments is that the shell/gravel sediment is formed in high energy conditions, whereas the shell bed of muddy sand forms in low energy conditions—an obvious difference, but one that has far-reaching implications so far as reworking and faunal type are concerned.

Sessile epifauna can live in either environment but shell/gravel grounds tend to support more epifauna than muddy sand environments where there are generally fewer suitable surfaces for attachment. Because of the different amounts of mud in the two environ-

ments, deposit feeders are more abundant in muddy sand, and suspension feeders more abundant in shell/gravel grounds.

We are now in a position to define in general terms the different ecological classes of animals to be found on, and in, different sea floors. Fine-grained sediments encourage the development of an infauna which consists mostly of deposit feeders; coarse-grained sediments support a community of infauna and epifauna which are mainly suspension feeders; rock surfaces support an epifauna of suspension feeders. Fine-grained sand is a poor medium for benthonic life and what little there is consists largely of infauna. Carnivores may inhabit all four environments.

Transportation. Work on the erosion and transport of sediments by Hjølstrom (1935) and Inman (1949) has demonstrated the comparative resistance of sediments of different grain sizes to erosion (see text-fig. 2). Fine-grained sand (of about 0.18 mm. diameter) marks the transition zone between transport in suspension and transport by surface creep. It is more easily moved than either the finer or the coarser grades of sediment and so tends to be better sorted. Although practically nothing is known of the behaviour of different grades of poorly sorted deposits in currents of different strengths, it is known that turbulence is greater over the rougher surfaces and that selective scouring must occur. Both Menard and Boucot (1951) and Johnson (1957) have discussed this problem in terms of sand and shells, and we assume that muddy sands and other ill-sorted sediments with shells will show a somewhat greater tendency to erosion (and shell concentration or removal) than the same sediments without shell material.

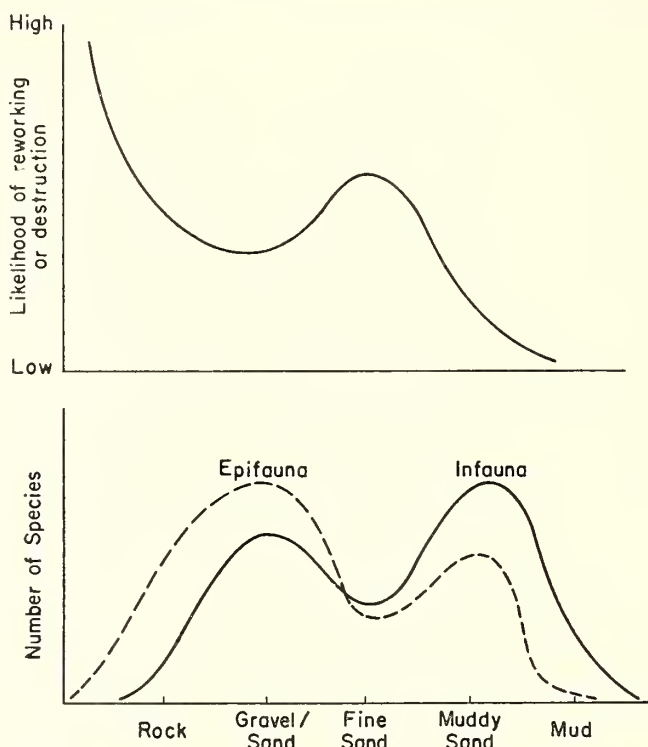
It is possible to generalize much of the information we have presented in the previous section. Text-fig. 2 shows the relationship between the abundance of epifaunal and infaunal species and the different grain sizes of sediment that they may inhabit. Since epifaunal species are more common in the higher energy environments and more exposed to currents, they are more likely to be transported after death. This is especially true of sessile epifauna. Active epifaunal species which inhabit areas of deposition are less likely to be transported after death. Only on sandy beaches are infauna more abundant than epifauna in a high energy environment.

One final point is of particular concern to palaeontologists. We have estimated the numbers of infaunal and epifaunal species which have hard parts and have therefore a chance of preservation as fossils in the Irish Sea. Out of a total of 79 of the more abundant species of infauna on the sea floor off the Isle of Man about 33 per cent. are preservable; out of a total of 56 of the more abundant species of epifauna 58 per cent. are preservable.

Influence of benthos on sediment. If a sediment is conducive to the establishment of life, then the character of the sediment will change. Burrowing organisms will modify existing sedimentary structures and create new organic structures by their burrowing activities and through digestion by deposit feeders and deposition of faeces; further, the increasing abundance of living and dead shelled animals will alter the texture of the sediment so that in extreme cases the sediment becomes a shell bed. The presence of organisms on the surface of the sediment affects its rate of accretion or erosion. At low current velocities, sedimentary particles may be trapped, but at higher velocities erosion may be prematurely induced or accelerated by the development of scouring around the shells. Experiments with shells in a flume tank have demonstrated this process (Johnson

1957). Indeed it is possible that the appearance of shells on a previously stable substratum could lead to its partial or even complete removal, without the need for any other change in the environment.

At the same time the change in the nature of the sediment will have an effect on the composition of the fauna. The larvae of those animals with a pelagic phase do not simply settle wherever they happen to be when the time for settlement arrives but show,



TEXT-FIG. 2. Idealized frequency distribution of infaunal and epifaunal species according to the nature of the substrate. The upper graph indicates the likelihood of transport or destruction of the benthos after death on the different substrates.

more or less, some power of selection. They respond to a suitable substrate and can delay settlement for some time until one is found (Wilson 1952, Smidt 1951, Thorson 1957). One of the stimuli affecting the settlement of many species is the presence of adults of the same species, and the successful settlement of some individuals may lead to the establishment of a larger population of that species. The build-up in the sediment of shells and their possible eventual transformation into a shell bed will have obvious effects on the fauna and may even lead to the complete change from an infaunal to an epifaunal community.

Palaeoecological implications. One aspect of the environment, the substrate, has been taken and its influence and effects on the benthos examined. Geologists understandably

tend to overemphasize the importance of the sedimentary environment since the other two important factors of salinity and temperature are not immediately obvious. The preoccupation in this paper with the substrate and its effects on the benthos should not blind the reader to the importance of these other factors.

We have shown that the chances of transportation of the shells of epifaunal species must be greater than those of infaunal species. From this it could be presumed that the chances of the destruction of epifaunal shells must also be greater. But epifaunal skeletons are usually stronger than infaunal skeletons and to this extent the balance is redressed.

It is difficult to arrive at an accurate estimate of the proportion of epifaunal to infaunal species. Thorson (1957) has shown that the number of epifaunal and infaunal species are much the same in the Arctic seas but that epifaunal species may greatly outnumber infaunal species in tropical waters. He estimates that overall, epifaunal species may be about four times as abundant as infaunal. The considerable reduction in the proportion of epifaunal species in polar water is the result of the excessively cold waters during the polar winters, and is not typical of the geological past. For this reason it seems that there should have been even more epifaunal species in the geological past and that they should form a high proportion of the preserved fossil record.

Epifauna may be found *in situ* in isolated cases in the geological record, principally at unconformities or disconformities and in bioherms. They will probably be more abundant than infauna (although reworked) on the rocks flanking and immediately above such structures, and in the earlier rather than the later stages of infilling of a basin. They will also occur more commonly in sediments of transgressing rather than regressing seas.

Another factor which influences the picture of the fossil state is the evidence, derived from the benthos of the Irish Sea, that even under favourable conditions of preservation between one-half and two-thirds of the major species of the benthos are *not* preservable as body fossils. More analyses of this kind are required from different environments but the results underline what every palaeontologist knows empirically, and emphasize all too clearly the difficulties to be faced in the reconstruction of the ecosystem of a fossil community. It would seem to be a whimsical fact that the fossil communities most likely to be preserved *in situ*—the infaunal—are most likely to have fewest members of the original living community preserved as fossils.

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UPPER ORDOVICIAN TRILOBITES FROM NORTHERN YUKON

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ABSTRACT. The trilobites *Robergia yukonensis* sp. nov., *Cryptolithoides*, and *Ampyxina salmoni* Churkin are described from the Road River Formation. They occur above the Ashgillian (Late Upper Ordovician) graptolite zone of *Dicellograptus complanatus* var. *ornatus* and below beds containing the graptolite *Climacograptus scalaris* var. *normalis* of possible earliest Silurian age. *Robergia* and *Cryptolithoides*, although widely distributed geographically, have hitherto been reported from only Middle or presumed Middle Ordovician beds, and as a result have been considered reliable indices of that series.

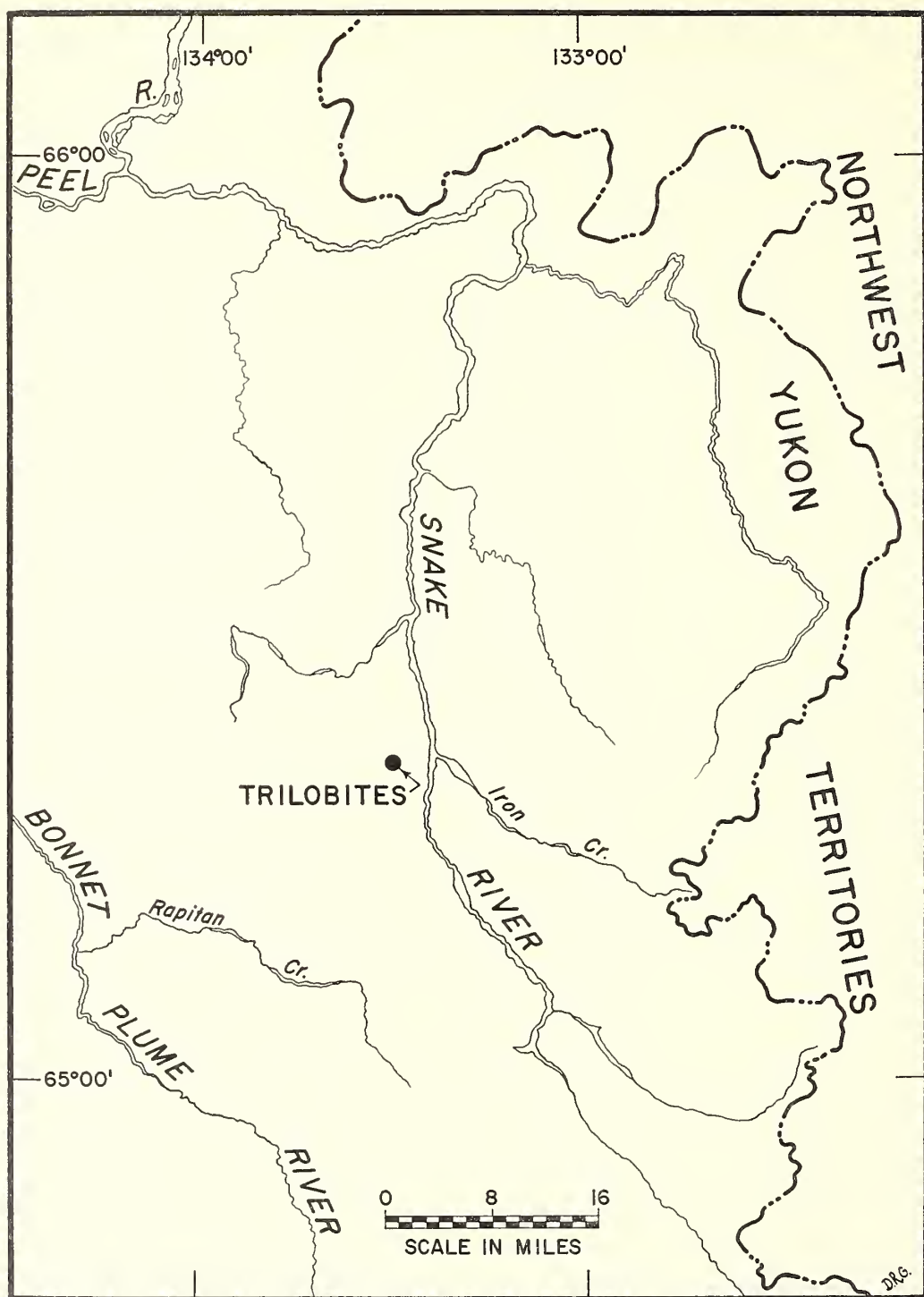
THE trilobite genera *Robergia*, *Cryptolithoides*, and *Ampyxina* were collected in 1963 from a 10-foot interval within the Road River Formation of northern Yukon Territory. *Robergia* and *Cryptolithoides*, although widely distributed geographically, have hitherto been reported from only Middle or presumed Middle Ordovician beds, and as a result have been considered reliable indices of that series. The *Ampyxina*, in association with *Toernquistia*? *idahoensis* and *Primaspis* sp., was described previously by Churkin (1963a) from a late Middle Ordovician graptolite shale in Idaho. In the same paper he noted that the presumably Middle Ordovician Caesar Canyon Limestone of Kay (1960) in Nevada has the same trilobites (*A. salmoni*, *T.*? *idahoensis*, and *Primaspis*) in association with *Robergia* and *Cryptolithoides*.

In the southern Northwest Territories, closer to the present study area, Lenz and Jackson (1964) listed *Robergia*, *Ampyxina*, *Cryptolithoides*, and other trilobites from possible late Middle or early Upper Ordovician beds containing ?*Orthograptus quadrimucronatus* (Hall). The trilobites were identified by R. J. Ross, Jr., who considered the presence of *Robergia* and *Cryptolithoides* as good evidence for a Middle Ordovician age assignment.

This paper first presents conclusive evidence, based on associated graptolites, of an extension in range of *Robergia*, *Cryptolithoides*, and *Ampyxina salmoni* into the Ashgillian (late Upper Ordovician), and then gives a formal description of the trilobites. The introductory section is by A. C. Lenz and the trilobite descriptions are by Michael Churkin, Jr.

LOCATION, STRATIGRAPHY, AND FAUNAS

The trilobites were collected just west of the Snake River, Yukon Territory (65° 21' N., 133° 30' W.; fig. 1) from a 10-foot shale and calcareous shale band approximately 30 feet below the top of the Road River Formation, which in this area ranges in age from Late Cambrian to Early Silurian. Graptolites were collected 10–20 ft. below, and 20–30 ft. above, the trilobites (fig. 2). The graptolites collected beneath the trilobites consist of *Dicellograptus* sp. (rare), *Orthograptus truncatus* var. *abbreviatus* Elles and Wood (fairly common), *Climacograptus supernus* Elles and Wood (fairly common), *Cl. hvalross* Ross and Berry (common), *Cl. hastatus* var. *martini* Ross and Berry (rare), *Cl. cf. raricaudatus* Ross and Berry (very rare), and *Glyptograptus* sp. In beds 20–30 ft.



TEXT-FIG. 1. Map of part of Yukon, showing trilobite locality.

above the trilobites, the graptolite *Climacograptus scalaris* var. *normalis* Lapworth occurs in considerable numbers.

AGE AND CORRELATION

The graptolite fauna which underlies the trilobites correlates with the *Dicellograptus complanatus* var. *ornatus* Zone of northern Yukon Territory (Jackson and Lenz 1962); this is indicated by the presence of *Orthograptus truncatus* var. *abbreviatus* and *Climacograptus superius*, both typical representatives of the Ashgillian *ornatus* Zone of Yukon. The fauna may also be correlated, at least in part, with the Ashgillian of Great Britain, the *Dicellograptus complanatus* Zone of the Basin and Range area of western United States (Ross and Berry 1963), and with the *Dicellograptus anceps* Zone of Idaho and Utah (Churkin 1963b). The overlying graptolite *Climacograptus scalaris* var. *normalis* ranges from uppermost Ordovician to lower Lower Silurian in Great Britain and elsewhere in northern Yukon, but because of its stratigraphic position in this section is possibly lowest Silurian.

It is therefore evident that the Ordovician trilobite genera *Ampyxina*, *Roergia*, and *Cryptolithoides*, while in this instance of Late Ordovician (Ashgillian) age, range through Middle and Upper Ordovician beds of the North American Cordillera.

SYSTEMATIC PALAEOLOGY

Family REMOPLEURIDIDAE Hawle and Corda

Genus ROERGIA Wiman

Roergia yukonensis sp. nov.

Plate 4; Plate 5, figs. 1-5.

Material. Collection consists of twenty-two specimens, mostly isolated cranidia. Four specimens are nearly complete, having thoracic segments and pygidia attached to cranidia. Holotype, G.S.C. no. 19864; paratypes, G.S.C. nos. 19865-71. Geological Survey of Canada, Ottawa.

Description. Opisthoparian trilobite characterized by glabella narrowing posteriorly, expanding between eye lobes and with long (sag.) tongue, three pairs of lateral glabellar furrows successively deeper posteriorly. Anterior glabellar furrows nearly straight. Middle furrows slightly convex forward. Posterior furrows nearly straight but posterior tips faintly deflected forward in holotype. Faint axial furrow in the frontal part of the glabella, accentuated in some crushed specimens. Prominent palpebral lobes start opposite the middle of the first glabellar lobes and end opposite the third glabellar lobes. Free cheeks widest (trans.) opposite eyes, with raised convex borders and bearing long (6-8 mm.+) tapering genal spines. Eye composed of many quadrate lenses. Occipital ring bears mesial tubercle on several paratypes (Pl. 4, specimen c; Pl. 5, figs. 1, 2, 5); apparently not preserved on other specimens. Thorax narrow and gently tapering posteriorly. Thorax of eleven segments. Pleurae transversely directed and terminating in small posteriorly directed spines. Deep pleural furrows start near anterior portions of pleurae and cross each pleuron diagonally. The second pleural furrow begins at the inner posterior corner of each pleuron and intersects the longer diagonal furrow at about

two-thirds of the distance from the axial furrow to the outer tip of the pleuron. Articulating half-ring, large, nearly equal to axial ring in size. Each axial ring, and to a lesser extent each corresponding axial half-ring, separated by two furrows into three transversely convex portions.

Pygidium length about equal to width. Axis extends close to posterior margin and connected to margin by narrow post-axial ridge. Five axial rings seen on holotype; pleural regions flat and with two pairs of broad ridges merging into the outer and middle pair of pygidial spines. Inner pair of pygidial spines much shorter and apparently without corresponding inter-pleural ridges.

Details of the external surface where preserved show very fine (about 11 ridges/mm.) parallel ridges. The ridges parallel the general shape of the cephalon and pygidium but run across the pleurae parallel to the exsagittal direction and form a transversally parallel pattern across the axial region of the thorax.

Measurements of type specimens are given in Table 1.

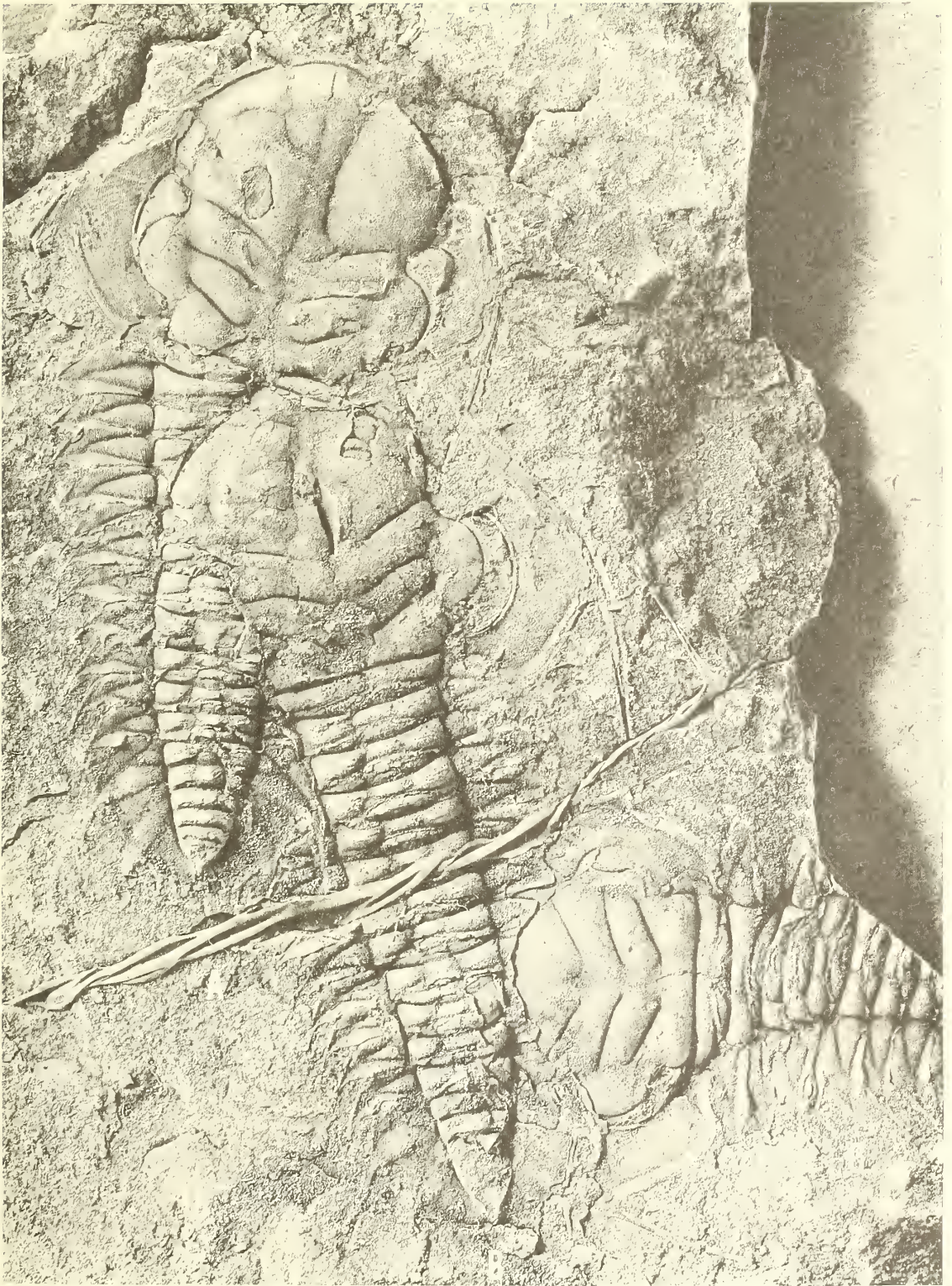
TABLE 1—*Robergia yukonensis* sp. nov.

G.S.C. no.	Holo- type	Paratypes					
	19864	19865	19866	19867	19868	19870	19871
Measurements in mm.							
Total length (sag.)	33.4	33.7	—	—	—	—	—
Length of cephalon (sag.)	12.7	12.3	—	—	—	11.6	5.1
Length of thorax (sag.)	14.7	15.4	—	—	—	—	—
Length of pygidium (sag.)	6.0	6.0	—	—	—	—	—
Maximum width of cephalon at base of genal spines (transv.)	17.6	—	16.5	—	—	—	—
Maximum width of cranium across palpebral lobes (transv.)	11.2	—	10.5	10.7	13.4	11.7	5.0
Length of palpebral lobes (exsag.)	3.7	3.6	3.4	3.7	4.0	3.4	1.8
Width of first axial ring (transv.)	—	5.6	5.4	—	—	6.2	—
Width of last (11th) axial ring (transv.)	3.4	3.6	—	—	—	—	—
Length of first pleuron (transv.)	3.7	—	3.7	—	—	3.9	—
Length of last pleuron (transv.)	2.8	3.5	—	—	—	—	—

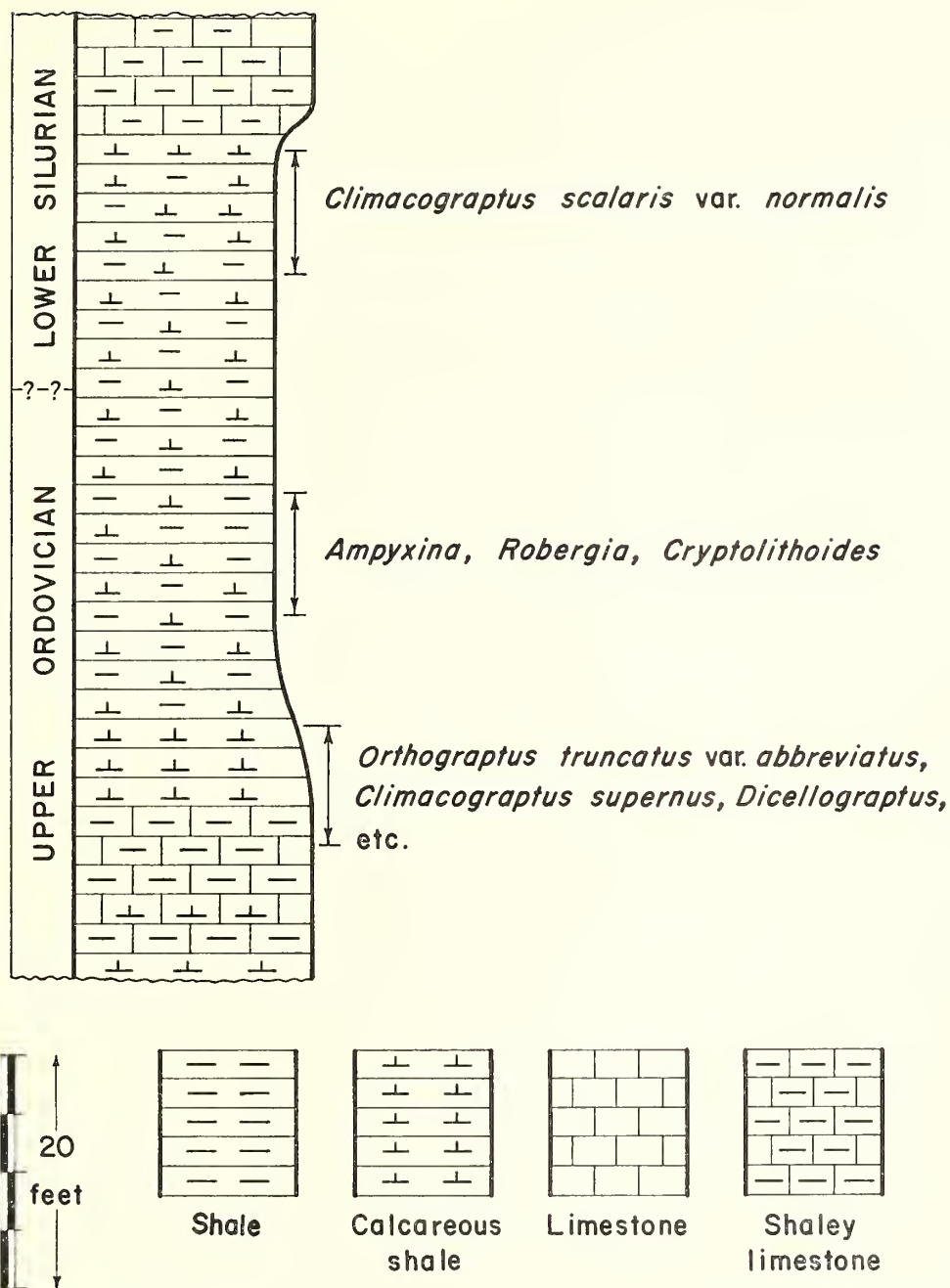
Discussion. The Yukon specimens broadly resemble *Robergia major* Raymond and *Robergia deckeri* Cooper from the southern Appalachians (Cooper, 1953; Whittington, 1959) but differ in the following ways: the glabellar furrows of *R. yukonensis* are less curved and are more posteriorly directed than in *R. major*, the middle glabellar furrow of *R. deckeri* is also more curved than in *R. yukonensis*, and the anterior end of the palpebral lobe lies behind the anterior glabellar furrow instead of directly opposite the glabellar furrow as in the Appalachian species. In *R. microphthalmus* (Linnarsson), the type species, the glabellar furrows are like those in the Appalachian species and differ

EXPLANATION OF PLATE 4

Robergia yukonensis sp. nov. ×4. A, holotype, G.S.C. no. 19864; B, paratype, G.S.C. no. 19865; C, paratype, G.S.C. no. 19866.



LENZ and CHURKIN, Ordovician trilobites



TEXT-FIG. 2. Section of part of Road River Formation, showing the relative occurrence of the graptolites and trilobites.

from *R. yukonensis* in the same way. In addition *R. yukonensis* has a faint axial furrow on its glabella that seems to be absent in other species of *Robergia*. Because of these differences the Yukon species is perhaps a derivative of *Robergia* as suggested by H. B. Whittington (personal communication) and could be considered a new genus.

In the thorax of *R. yukonensis* the pleural furrows, beginning at the inner posterior corners of each pleuron, intersect the longer diagonal furrows about two-thirds of the distance from the axial furrow, more than twice as far out on the pleuron from the axial furrow as in *R. deckeri*. Thus in *R. deckeri* the two sets of pleural furrows form small triangular nodes next to the axis, whereas in *R. yukonensis* most of the area of each pleuron is bounded by the same furrows.

In rare specimens possessing free cheeks the angle between the genal spine and the posterior border in *R. yukonensis* is more acute than that in the Appalachian species.

Occurrence. *Robergia* is a widespread genus that has been reported from North America, Europe, and Asia (see fig. 3). Fortunately, graptolites found in most of the *Robergia*-bearing sequences can accurately date each occurrence.

In the United States *Robergia* has only been recorded from Middle Ordovician rocks, and the National Research Council Ordovician Correlation Chart for North America (Twenhofel 1954) shows it as an important index fossil for the Black River and lower Trenton Stages (approximate equivalents to the lower half of the Caradoc Series in Great Britain).

The oldest reported occurrence of *Robergia* is from the upper part of the middle Table Head Formation of Newfoundland that is considered by Whittington and Kindle (1963) as lower Llanvirnian.

In Yukon Territory the genus occurs directly above Ashgillian graptolites possibly equivalent to the zone of *Dicellograptus anceps* and thus extends the range of *Robergia* to include highest Ordovician.

Family TRINUCLEIDAE Hawle and Corda

Genus CRYPTOLITHOIDES Whittington

Cryptolithoides sp. indet.

Plate 5, figs. 6–8

Material. Three fragmentary cephalae.

Description. Cephalon subrectangular in outline and characterized by antero-lateral angulation of cephalic margin. Glabella strongly convex, clavate, and smooth. Genae (cheek lobes) without ornamentation. Fringe narrows anteriorly, increasing in width

EXPLANATION OF PLATE 5

Figs. 1–5. *Robergia yukonensis* sp. nov., paratypes. 1, cranium $\times 4$, G.S.C. no. 19867; 2, cranium $\times 4$, G.S.C. no. 19868; 3, a nearly complete cephalon lying on a thorax with the pygidium attached $\times 2$, G.S.C. no. 19869; 4, cranium with part of the thorax attached $\times 2$, G.S.C. no. 19870; 5, small cranium $\times 4$, G.S.C. no. 19871.

Figs. 6–8, *Cryptolithoides* sp. indet. 6, half of a cranium showing the pattern of pits $\times 5$, G.S.C. no. 19872; 7, incomplete cranium $\times 4$, G.S.C. no. 19873; 8, external mould of cranium showing strongly convex and clavate glabella $\times 4$, G.S.C. no. 19874.

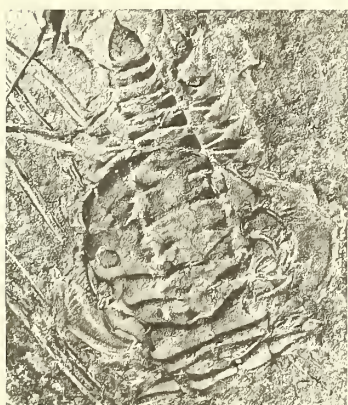
Figs. 9–12, *Ampyxina salmoni* Churkin. 9, nearly complete specimen with long genal spines and small glabellar spine $\times 4$, G.S.C. no. 19875; 10, incomplete specimen with thorax and pygidium attached to cephalon $\times 4$, G.S.C. no. 19876; 11, pygidium $\times 2$, G.S.C. no. 19877; 12, cranium $\times 4$, G.S.C. no. 19878.



1



2



3



4



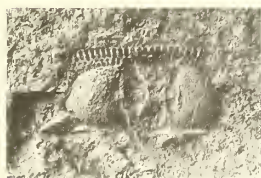
5



6



8



7



11



9



10



12

antero-laterally and postero-laterally. Pits in the fringe numerous. One row of pits external to girder. The outermost row of pits (E_1) in concentric and radial arrangement with the second row (I_1) except at the posterior lateral margin where the pits of the second row (I_1) decrease in size and are not paired with the outer pits. Anteriorly,

SYSTEM SERIES	STAGES	NORTHEASTERN	EUROPE-Ogygi-	NEWFOUNDLAND-	SOUTHEASTERN	SOUTH-CENTRAL	WESTERN	YUKON
		U.S.S.R.-Kharkin- dzhin and Darpir Fms. (Chugaeva et al. 1964, p. 18, 29, tables 3 and 8)	caris shales (Whittington, 1950, p. 543)	Table Head Fm. (Whittington and Kindle, 1963)	U.S.A.-Edinburg Fm. and equiv- alents (Cooper, 1953)	U.S.A.-Viola Ls. (Decker, 1933)	U.S.A.- Caesar Canyon Ls. (Churkin, 1963a)	TERRITORY, CANADA- Road River Fm. (this paper)
ORDOVICIAN	UPPER	ASHGILL						
	MIDDLE	CARADOC						
		LLANDEILO						
		LLANVIRN						
	LOWER	ARENIG						

TEXT-FIG. 3. Range of *Robergia* based on the ages of associated graptolites.

well-defined radial ridges separate the radially paired outer two rows of pits. Anterior of the glabella two more rows of pits (I_2 and I_3) in radial arrangement with the outer two pits but postero-laterally the pits inside the outer two rows irregularly arranged.

Discussion. Only fragmentary specimens were collected, but no significant differences could be found between the Yukon material and *C. ulrichi* (Whittington, 1941). The size of the Yukon specimens, length (sag.) 3–4 mm., width (trans.) 7 mm., falls within the range of the smaller cephalae described by Whittington.

Occurrence. *C. ulrichi* occurs in the Viola Limestone of Trenton age (equivalent to part of the upper half of the Caradocian) in Oklahoma, and the genus is reported from Ordovician rocks in Texas (Whittington 1941). More recently, *Cryptolithoides* has been reported from the western U.S. where it occurs in the Caesar Canyon Limestone of the Toquima Range, Nevada, (Kay 1960) and in the Middle (?) and Upper Ordovician Hanson Creek Formation of the Seetoya Mountains, Nevada (Kerr 1962). In the Caesar Canyon Limestone, *Cryptolithoides* is associated with *Ampyxina salmoni*, *Robergia* cf. *major*, *Toernquistia*? *idahoensis*, *Primaspsis* sp. and *Flexicalymene* sp., a trilobite fauna much like that from graptolitic shale of Trenton age in central Idaho that is correlated (Churkin 1963a) with the Caradocian graptolite Zones (11) of *Climacograptus wilsoni* and (12) of *Dicranograptus clingani*. *Cryptolithoides* thus ranges from Trentonian (Caradocian) in the southern United States, its type area, into Ashgillian in Yukon and may have a range of Caradocian through Ashgillian in the western United States.

Family RAPHIOPHORIDEA Angelin
Genus AMPYXINA Ulrich

Ampyxina salmoni Churkin

Plate 5, figs. 9–12

1963a *Ampyxina salmoni* Churkin, pp. 424–5, pl. 51, figs. 1–10.

Material. Four complete specimens, six cranidia, and seven pygidia.

Description. The specimens under study agree in all essential respects with *A. salmoni* originally described from Ordovician graptolitic shale in central Idaho (Churkin 1963a). The Idaho collection consists of several hundred specimens, none of them as complete as those from Yukon, and the new material makes possible the following additions to the original descriptions.

Free cheeks apparently very narrow, lying along steeply flexed lateral margins of fixigenae. The long genal spines extend smoothly backward as continuations of curved cephalic margins. The spines gently curve inward, taper slightly, and extend well past the pygidium.

Thorax with five segments. Axis about one-fifth total width. Pleurae extend out horizontally but flexed downward at distal ends. Interpleural furrows extend from anterior edges of pleurae next to axial furrows and cross pleurae obliquely toward lateral margins. Furrows become deeper and broader distally. Pleural furrow of first segment curved convexly forward, on succeeding segments less curved and nearly straight across fifth segment. Distal ends of pleurae separated from each other by small notches that produce a serrated margin.

Dimensions. G.S.C. no. 19875: total length (sag.) 7.7 mm., length (sag.) of cephalon 2.9 mm., length of thorax (sag.) 2.4 mm., length of pygidium (sag.) 2.4 mm., width of cranidium at posterior margin 6.9 mm., maximum width of glabella 2.3 mm., width (trans.) of pygidium at anterior end 6.6 mm., length of genal spine 5.3 mm. +.

Discussion. The Yukon specimens possess the straight pygidial ribs characteristic of *Ampyxina salmoni* instead of backward flexed ribs as in the very similar *A. bellatula* (Savage) illustrated by Whittington (1950, 1959) and *A. powelli* (Raymond) described by Cooper (1953) and Whittington (1959). In addition, the first interpleural furrow in the Yukon specimens appears less curved forward than in *A. bellatula* or *A. powelli*.

Occurrence. Type *Ampyxina salmoni* is from the type locality of the Saturday Mountain Formation of central Idaho where it is associated with graptolites equivalent in age to the Caradocian Zones 11 and 12 of Elles and Wood (Churkin 1963a). The writer has identified *A. salmoni* from the Caesar Canyon Limestone of the Toquima Range, central Nevada (Kay 1960; Kay and Crawford 1964) where it is found with *Robergia* cf. *R. major* and *Cryptolithoides* sp., an association similar to that in Yukon. *A. salmoni* occurs in Middle Ordovician (Caradocian) rocks in both Idaho and Nevada and is found in considerably younger Upper Ordovician (Ashgillian) rocks in Yukon.

Ampyxina is a widely ranging genus as it has been reported from the early Middle Ordovician (Porterfield–Wilderness Stages) of Virginia, Alabama, Tennessee (Cooper 1953; Whittington 1959), and the Upper Ordovician of Missouri and Illinois (Rowley 1909; Savage 1917).

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SILURIAN *GIRVANELLA* FROM THE WELSH BORDERLAND

by HAZEL M. JOHNSON

ABSTRACT. A general survey of the calcareous algae from Silurian limestones of the Welsh Border has yielded many algal remains particularly of the genus *Girvanella*. Nine species of this genus are here described, eight of which are new; and they are grouped according to their size and mode of growth. The Sarmenta group includes three new species, *G. sarmenta*, *G. fragila*, and *G. proluxa*; the Problematica group two new species, *G. pusilla*, *G. incompta* as well as *G. problematica* and its var. *lumbricalis*; the Media group with one new species *G. media*, and the Ramosa group two new species *G. ramosa* and *G. effusa*. The basis for subdividing the genus is given and the distribution of the specific forms in the varied lithology of the limestones are recorded.

A GENERAL survey of the calcareous algae present in the Silurian limestones of the Welsh Border has shown that algae are more abundant and widespread than has hitherto been recorded. Specimens were collected from numerous localities within the area demarked approximately by Wenlock Edge to May Hill and Dudley to Old Radnor (text-fig. 1).

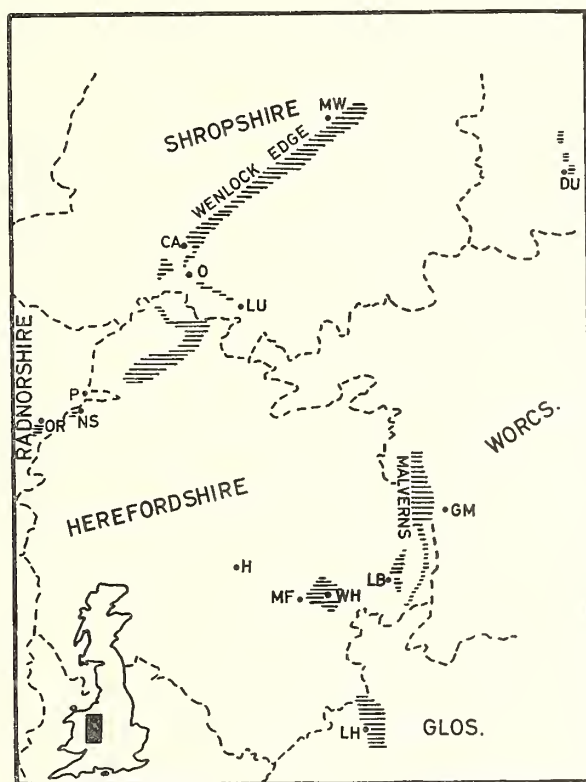
Previous records of algae in this area are few and the belief that algae contributed to the formation of reef limestones was largely unproved. From the Woolhope Limestone, Garwood and Goodyear (1918) described algal limestones at Old Radnor and Nash Scar; also Garwood (1931) mentioned an undescribed *Solenopora* at Woolhope. *Girvanella* is not recorded by Squirrel and Tucker (1960) in an account of the geology of the Woolhope Inlier.

For the Wenlock Limestone, Wethered (1890, 1893) described algae at May Hill, Ledbury, and Purley (West Malverns). Chapman (1907) and Crosfield and Johnston (1914) recorded algae or algal fragments at Dudley. Several authors have indicated the presence of algal limestones as opposed to brachiopod, crinoid, or other facies at Wenlock Edge but no details of localities were given. Furthermore they supposed that masses of algae together with corals and stromatoporoids were engaged in the building of the Ballstones (Hill 1936, Butler and Oakley 1936, Whittard 1952). Likewise the Crog Balls (found at Dudley) were believed by these authors to be the result of algal decomposition. As far as is known there have been no published records of calcareous algae obtained from the Bringewood Beds (Aymestry Limestone) of this area.

Only a very few of the published accounts mention the genus *Girvanella*. *G. problematica* recorded by Wethered (1890, 1893) was asserted by Garwood (1931) to be '*Sphaerocodium* *munthei*' which is now recognized as an association of *Rothpletzella* and *Wetheredella* (Wood 1948). *G. conferta* (Chapman) appears to belong to the genus *Rothpletzella* as it possesses dichotomous branching. The only other record was by Crosfield and Johnston (1941) who noted the presence of algal fragments in the Crog Balls of the Wren's Nest, Dudley, but gave no evidence to show whether they belong to the genus *Girvanella*.

When the present research began, there was little known about Silurian calcareous algae of the Welsh Border and no *Girvanella* records were identified to the species. The

commonest algal genus, *Girvanella*, was found to vary so much that it did not appear valid to retain all variants at generic level, or to regard them as related to the Ordovician type, *G. problematica*. It seems possible that the species of Silurian filamentous algae were numerous and also similar forms could associate together as do living



TEXT-FIG. 1. Reference map of the Welsh Border showing the important areas for *Girvanella*. CA, Craven Arms; DU, Dudley; H, Hereford; GM, Great Malvern; LB, Ledbury; LH, Longhope; LU, Ludlow; MF, Mordiford; MW, Much Wenlock; NS, Nash Scar; O, Onibury; OR, Old Radnor; P, Presteign; WH, Woolhope.

forms today. Slight dissimilarities in filament character would not necessarily be reflected in the fossils although several different types of filamentous algae have been proved.

The genus *Girvanella* is subdivided here on filament size and mode of growth which includes branching habit, encrusting and non-encrusting, attached and free forms, the constancy of tube diameter, curvature of tubes, and the amount of adherence between tubes. Several species have similar modes of growth and are grouped together. They can be distinguished by their filament size. A full account of these and other algae can be found in Green (1955, 1959).

METHODS OF SAMPLING AND EXAMINATION

The presence of *Girvanella* was rarely found to be indicated by macroscopic structures in the limestones investigated so a suite of specimens from each exposure was examined. Specimens were also taken at intervals along bedding planes. Particular attention was directed to beds in the neighbourhood of reef or reef-like structures where changes in the character of the limestone were likely to be rapid. Thin sections were found to be the most satisfactory for the study of the algae. Measurements on algal material were made by using camera lucida drawings mostly at magnifications of $\times 350$ and $\times 600$. The accuracy of this method was checked by measurements from photographs and also by direct measurements using an eyepiece micrometer scale.

The method used to determine the diameter of algal filaments was to measure the internal diameters of five tubes per specimen to give the range of variation and probable mean. With indistinct groups, the variation is greater, due to increased error in measurement. Longitudinal sections of the tubes were found to be more satisfactory in giving the true diameter. These were compared with tubes seen in cross-section as in the method used by Wood (1957, 1963), but Wood's method was found to be less accurate when measuring finer filaments of $5\ \mu$ or less in diameter. Furthermore it was difficult to distinguish transverse and oblique sections especially in fine tubes with thick walls or curving filaments when applying Wood's technique. In many sections the position of the original wall is marked by the greatest concentration of calcite dust (Wood 1941) against the clear calcite of the lumen, and, except in indistinct groups, this darker concentration of dust can be used to determine the original diameter of a filament. This criterion has to be used with caution however, for the calcite dust of the wall may partly obscure the clear lumen in some longitudinal sections.

Crushing of an algal filament is unlikely to occur before death owing to its internal pressure. Flattening only appears to occur when tubes are adherent to each other and nearly always in encrusting forms where the filaments are in a felted mass. Where crushing has occurred, the clarity of the wall disappears and this gives a good indication of the doubtful value of any measurements taken.

The number of each species of *Girvanella* examined by the above method is as follows: 3 specimens of *G. problematica* var. *lumbricalis*, 40 *G. effusa*, 60 *G. ramosa*, 70 *G. fragila*, 85 *G. media*, 95 each *G. sarmenta* and *G. prolixa*, 115 *G. pusilla*, 125 *G. incompta*, and 160 *G. problematica*.

MORPHOLOGY AND SYSTEMATIC POSITION OF THE GENUS

Class POROSTROMATA Pia 1927 ex Harlan Johnson 1959

Genus GIRVANELLA Nicholson and Etheridge 1878

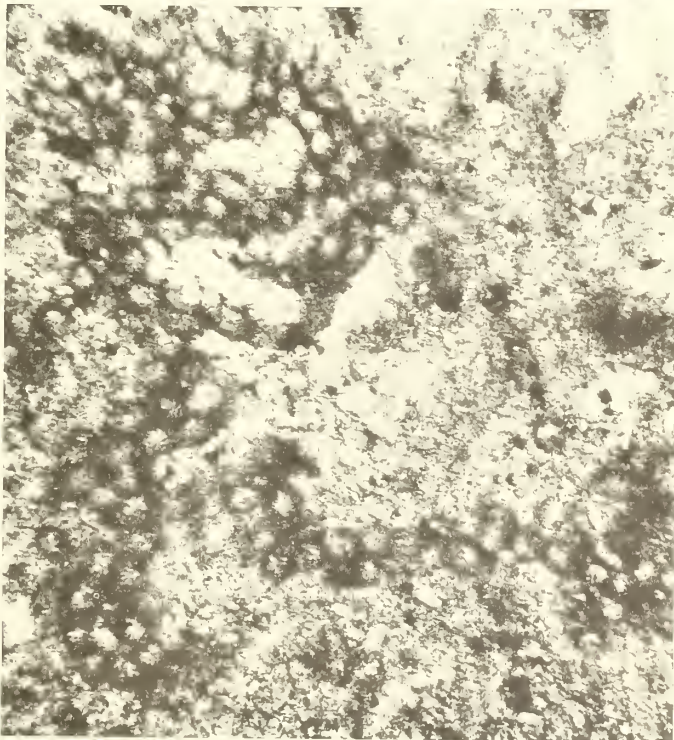
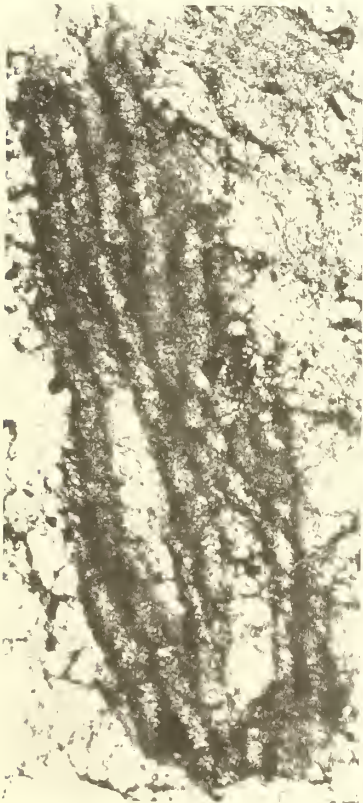
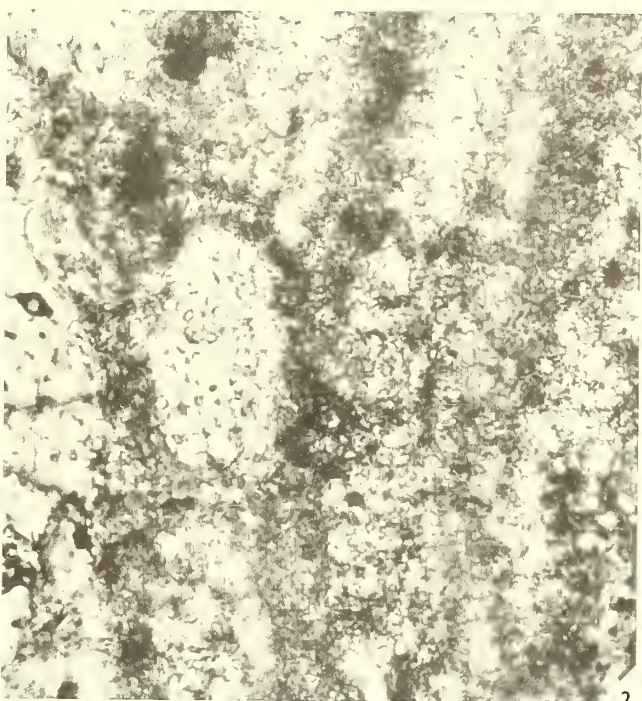
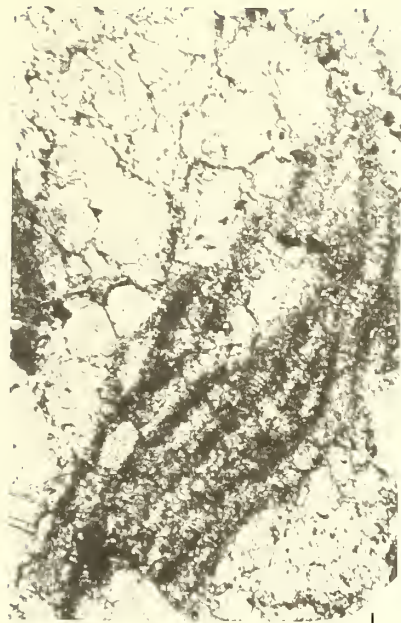
Type species. Girvanella problematica Nicholson and Etheridge.

EXPLANATION OF PLATE 6

Figs. 1, 2. *Girvanella* cf. *prolixa* sp. nov., showing septation and possible heterocyst. MF 1, Woolhope Limestone, GSM. PF 2838/1. 1, $\times 220$. 2, enlarged view $\times 1000$.

Fig. 3. *G. prolixa* sp. nov. with septate filaments. MF 1, Woolhope Limestone, GSM. PF 2837/5; $\times 220$.

Fig. 4. *G. sarmenta* sp. nov. Tubes seen in cross-section. WE 11, Wenlock Limestone, GSM. PF 2845/2; $\times 180$.



3

4

Original Diagnosis. 'Nodules composed of microscopic tubuli, with arenaceous or calcareous (?) walls, flexuous or contorted, circular in section, forming loosely compacted masses. The tubes apparently simple cylinders, without perforations in their sides, and destitute of internal partitions of a similar kind.' Wood (1957) in his re-description of the type species of *Girvanella* does not give a formal emended diagnosis of the genus.

Description. The original diagnosis gave the tube diameters as $10\ \mu$ and $18\ \mu$ but later descriptions have considerably extended this range of diameter (Wethered 1889-93, Høeg 1932, Wood 1957, Johnson *et al.* 1959). During this investigation Silurian members of the genus *Girvanella* were observed to have a range in diameter from 2 to $31\ \mu$. All the filaments examined had the fine granular calcite 'dust' wall (Wood 1941), which was occasionally iron stained, and enclosed a lumen of clear calcite crystals. Aggregations of opaque iron ores including pyrite were found within the lumen in some specimens. The mode of growth was found to be variable. The specimens investigated ranged from parallel sets of filaments having each tube of even diameter throughout to highly contorted filaments with variable diameters; from a loose non-adherent arrangement of tubes to tubes in contact or adherent to each other; from no branching to highly branched forms; and from free living, possibly floating plants to attached forms, encrusting or associating in composite growth with other algal genera. Another feature not recognized in the original diagnosis is one of possible septation (Pl. 6, figs. 1-3).

Definite reproductive organs are unknown within the genus and this may also be the result of indifferent preservation or that the main method of reproduction was by fragmentation of the filaments. A possible 'heterocyst' has been found in one instance with a general rounding of a septate filament which did not appear to be a cut branch as no fracturing of the clear lumen was visible. The 'heterocyst' was oval in shape (Pl. 6, figs. 1, 2) and appeared to be an integral part of the filament rather than a protuberance from it.

From the evidence stated in the foregoing paragraphs it would appear that the formal diagnosis of the genus *Girvanella* requires some revision. Since, however, it is the purpose of this contribution to describe the Silurian species of *Girvanella*, a discussion of the Ordovician type material is not included. The genus *Girvanella* is used in this work in agreement with previous workers though it is suggested that later studies may well lead to subdivision of the genus.

Lower Palaeozoic species and varieties. Høeg (1932), in describing the Ordovician algae from the Trondheim area, subdivided *Girvanella problematica* into three varieties by differences in size and habit, viz. vars. *typicalis*, *moniliformis*, and *lumbricalis*. In 1942 Lewis reviewed the various Ordovician *Girvanella* and concluded that they were all varieties of *G. problematica* including his new variety *G. spiralis* from the Lévis group, Quebec, and *G. ocellata* which had been described by Seely (1885) under the genus *Strophochetus*. Silurian *Girvanella* have not been similarly subdivided and the present work has shown that they have a different range of form from their Ordovician counterparts. *Girvanella* from the Welsh Borderland was found to be divisible into eight distinct growth types as follows:

1. Sets of parallel or sub-parallel filaments of apparently unlimited growth, at least

- partly adhering to each other as in the *G. problematica* var. *moniliformis* Høeg (1932) or as faggot-like bundles.
2. A loose coiling of filaments as in *G. problematica* (redefined by Wood 1957), or more specifically in a coil (as in *G. problematica* var. *typicalis* Høeg 1932). Branching here is infrequent, absent, or in limited portions only.
 3. Short curved loose filaments, sparsely branched, sometimes encrusting, corresponding in form to *G. problematica* var. *lumbricalis* (Høeg).
 4. A spiral development of a single filament (or a few filaments) as in var. *spiralis* (Lewis).
 5. Tight coiling of the filaments within a group. This is usually the result of adhering, much branching, curving filaments.
 6. Highly branched, curved filaments with uneven diameter, not strictly in a coil but matted together.
 7. A 'raft'-like development, probably a variety of the parallel tubes growth form (1) but where the filaments are of approximately equal length and appear to be of limited growth. Tubes are adherent.
 8. Encrusting forms which may be one or more of the above growth forms.

The tube diameter of these growth forms were also compared and from this data subdivision into district species was found to be possible. Four species groups have been erected for the Silurian *Girvanella*.

Group A SARMENTA (growth form 1 and rarely 7)

Description. Groups of parallel filaments mostly adherent to each other. In longitudinal section appearing as long tubes (tubes of indefinite length), mainly in contact, unbranched or with scarcely any branching. In transverse view the circular cross-sections are arranged in clusters.

Remarks. Normally, no indications of any attachment to substratum are visible. Only in a few specimens do the tubes appear to arise from one end. Raft-like forms are at present included as smaller specimens of this group. Division into species within the group is on the internal diameter of the tube, which varies from 2 to 31 μ .

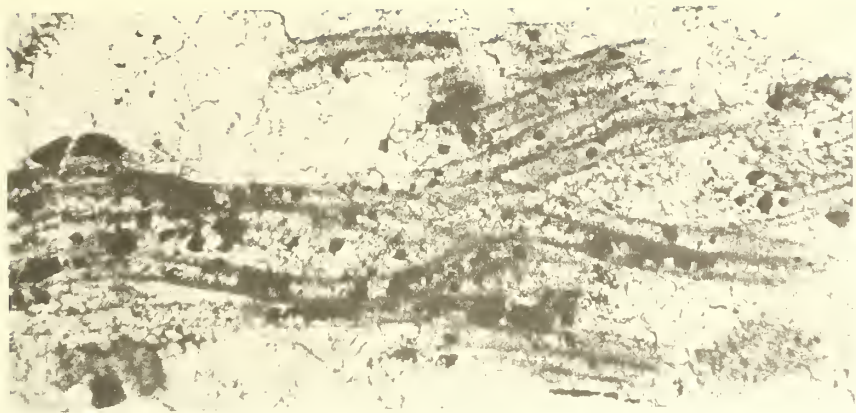
Species. *Girvanella sarmenta* sp. nov., *G. proluxa* sp. nov., *G. fragila* sp. nov.

Group B PROBLEMATICA (growth forms 2, 3, 4, sometimes 8)

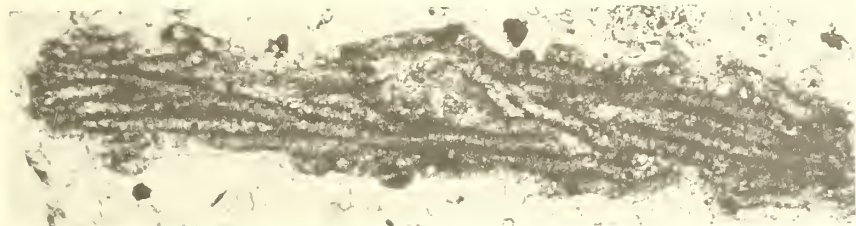
Description. Loosely coiling or tangled groups. Tubes mostly not in contact with each other. Branching infrequent or none. Tubes do not lie parallel or if they attain a sub-parallel direction they are mostly not adherent to each other.

EXPLANATION OF PLATE 7

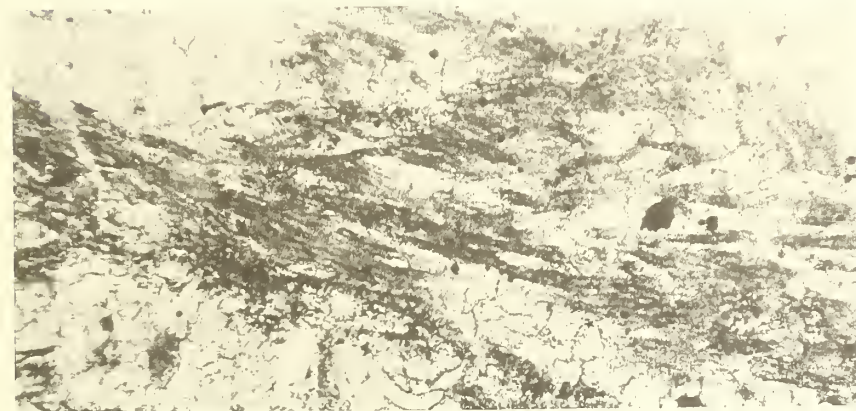
- Figs. 1, 2. *Girvanella sarmenta* sp. nov. 1, Holotype; only part of specimen figured. Length of specimen 2.6 mm. Tubes elongate and of even diameter. WE 15, Wenlock Limestone, GSM. PF 2846/4; $\times 160$.
2, Paratype; WE 15, GSM. PF 2846/3; $\times 140$.
- Figs. 3-5. *G. fragila* sp. nov.; MF 1, Woolhope Limestone. 3, 4, Holotype; different sections of the same specimen (figs. not in alignment); GSM. PF 2839/1. Length of specimen 2.5 mm.; $\times 140$.
5, Paratype; specimen with slightly larger tubes, GSM. PF 2837/1; $\times 180$.



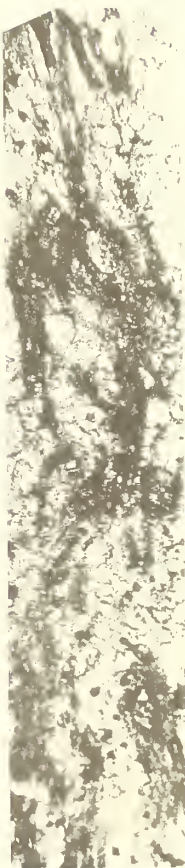
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Remarks. Internal diameter of tubes ranges between 2 and 28 μ . Branching occurs more frequently in the larger forms. Also in the larger forms, the tubes tend to be more adherent to each other than in the finer-tubed specimens. A variation of this is a tight coiling of filaments of even diameter over each other. The extreme variety of this is the production of a spiral form usually by one filament.

Species. *G. problematica*, *G. pusilla* sp. nov., *G. incompta* sp. nov. (probably including *G. problematica* var. *spiralis* Lewis). *G. problematica* var. *lumbricalis* may represent a distinct species (growth form 3).

Group C MEDIA (growth form 5, sometimes 8)

Description. Groups of filaments tightly coiling and adhering branching clusters. Branching fairly frequent. Tubes even diameter throughout with apparently no constrictions. Internal diameter 8–18 μ .

Species. *G. media* sp. nov.

Group D RAMOSA (growth form 6, sometimes 8)

Description. Forms characterized by highly branched adherent tubes usually in clusters. Branching irregular. Tubes uneven in diameter and length between branches short.

Remarks. Constrictions are often visible. Groups are sometimes encrusting. The internal diameter range is usually between 11 and 27 μ , rarely more. The group is distinguished from *G. media* by its irregular diameter and more frequent branching and by its irregular type of branching from the dichotomous branching of a *Rothpletzella*.

Species. *G. ramosa* sp. nov., *G. effusa* sp. nov.

SPECIES DESCRIPTIONS

Group SARMENTA

Girvanella sarmenta sp. nov.

Plate 6, fig. 4; Plate 7, figs. 1, 2; text-fig. 3g

Diagnosis. A non-encrusting *Girvanella* with bundles of parallel, even diameter tubes with no constrictions. Tubes seldom branch and are mostly adherent to each other. Filament, or internal tube diameter 18–31 μ , the majority having diameter between 19 and 22 μ .

Holotype. GSM. PF 2846/4; Plate 7, fig. 1. Wenlock Limestone, Silurian. Wenlock Edge, WE 15(5), SO 856455.

Paratype. GSM. PF 2846/3; Plate 7, fig. 2. Same locality and horizon.

Description. This species is one of the largest *Girvanella* found in these Silurian limestones. Within the Sarmenta group, the narrowest diameter tubes of this species just overlap the range for *G. prolixa*, but the mean value for the filaments is 5 μ greater. It also appears to correspond to the Ordovician *G. problematica* var. *moniliformis* (Høeg) in size and longitudinal view but differs from it in transverse section in having tubes arranged in clusters and not in a single row.

There does not appear to be any marked tapering to one end of a cluster so there is no evidence of this form being attached to a substrate.

Distribution. Woolhope and Wenlock Limestones of the Woolhope Inlier and Wenlock Edge. It is infrequent in the Woolhope Limestone. Most specimens have been found at the south-west end of Wenlock Edge although it has been found at the other localities in the Wenlock Limestone on the Edge and at Fownhope.

Girvanella prolixa sp. nov.

Plate 6, fig. 3; Plate 8, figs. 2-4; text-fig. 3d

Diagnosis. *Girvanella* occurring in small groups of parallel tubes, mostly adhering, sometimes free. Filaments long, with circular cross-section, even diameter and nearly straight. Range of filament diameter 12-18 μ , occasionally more. Most filaments are between 14 and 16 μ wide.

Holotype. GSM. PF 2840/2; Plate 8, fig. 2. Grey Measures, Wenlock Limestone. Silurian. Farley Quarry, north of Much Wenlock, Wenlock Edge, Shropshire WE 3(7), SJO 15629.

Remarks. Specimens examined from the Wenlock Limestone at Fownhope were found to have tube diameters mostly between 17 and 18 μ wide, which is slightly larger than average. The Fownhope district appears to have been favourable for calcareous algae so it is possible that some algal growths may have been better developed than elsewhere. Some specimens from Fownhope show possible septation in the tubes (Pl. 6, figs. 1-3).

In a very few cases, the filaments partly converge at one end, which could indicate that some of these plants may have been attached during life. Another indication of this may be the 'rafts', shorter length groups which may have formed either part of a larger group or an early stage. In some, the adherent tubes converge to a narrow region and end either by the tubes joining or overlapping.

Distribution. The Woolhope and Wenlock Limestones of the Woolhope Inlier and the Wenlock Limestone of Wenlock Edge. It is occasional in the Woolhope Limestone at Mordiford, but is more common in the Wenlock Limestone. It is abundant in the Grey Measures of Wenlock Edge near Much Wenlock and to the north-east although it has been obtained from most of the exposures examined along the Edge.

Girvanella fragila sp. nov.

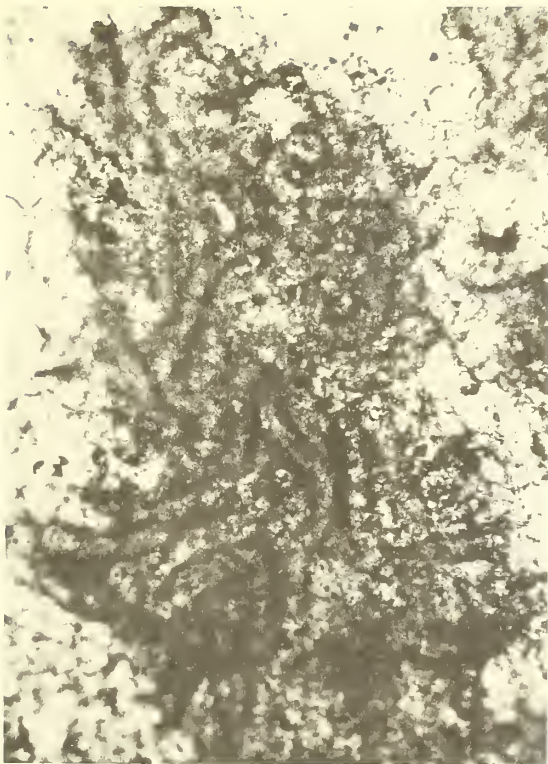
Plate 7, figs. 3-5; text-fig. 3a

Diagnosis. *Girvanella* in which the tubes are parallel, of even diameter in bundles, mostly adherent, occasionally partly free. Tubes long, straight or slightly undulating. Branching

EXPLANATION OF PLATE 8

Fig. 1. *Girvanella media* sp. nov. Small cluster branching tubes mostly adjoining tubes in contact. FH 2, Wenlock Limestone, GSM. PF 2841/3; $\times 250$.

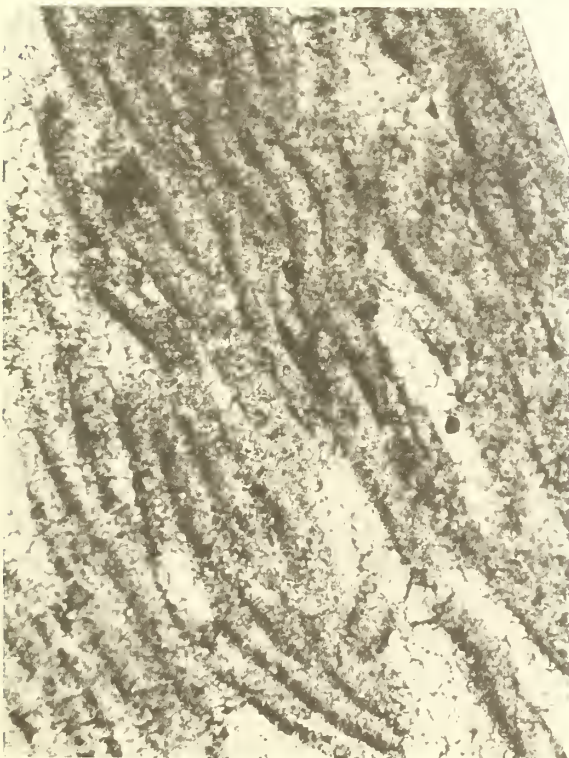
Figs. 2-4. *G. prolixa* sp. nov. 2, Holotype showing sub-parallel tubes, slight branching; WE 3, Wenlock Limestone, GSM. PF 2843/1; $\times 200$. 3, Specimen with sub-parallel tubes slightly larger than average; FH 2, Wenlock Limestone, GSM. PF 2840/2; $\times 250$. 4, Transverse section of tubes; MF 1, Woolhope Limestone, GSM. PF 2837/6; $\times 260$.



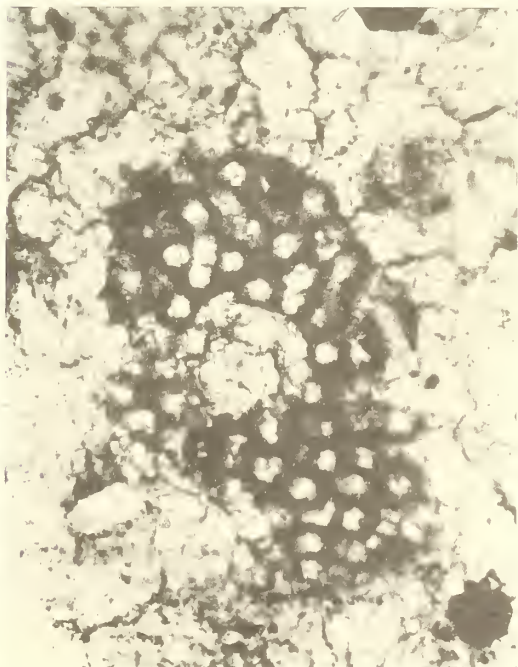
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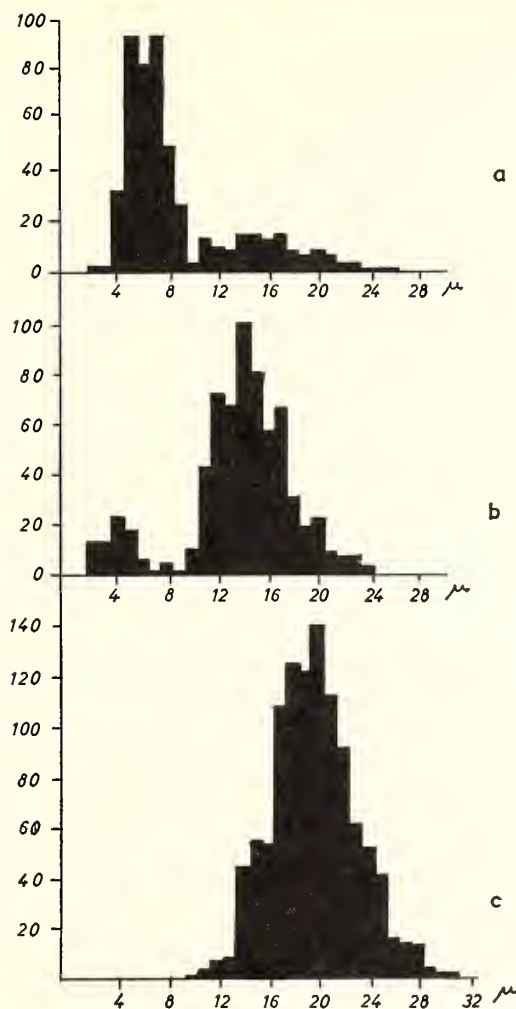
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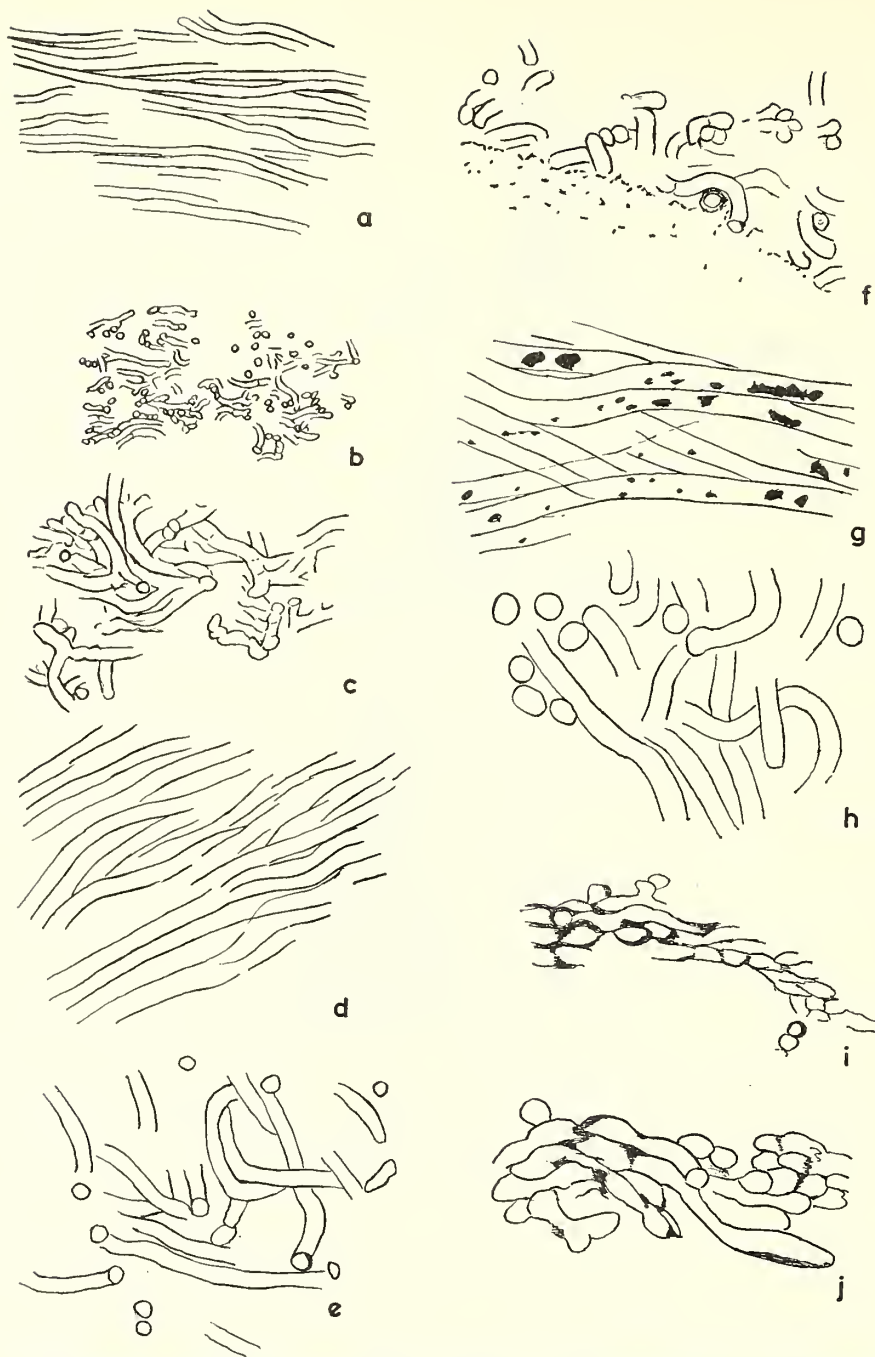
TEXT-FIG. 2. Range of diameter of *Girvanella* tubes from Mordiford, Fownhope, and Wenlock Edge. Five measurements were taken from each *Girvanella* specimen, thus giving the variation for each group and also more overlap of sizes than if the mean only is used. *a*, Mordiford, 148 specimens measured; *b*, Fownhope and *c*, Wenlock Edge, 162 and 164 specimens respectively.

rare. Internal diameter of tubes range from 2 to 9 μ , mostly 5–7 μ , very occasionally to 10 and 11 μ .

Holotype. GSM. PF 2839/1; Plate 7, figs. 3, 4. Woolhope Limestone, Silurian small exposure at junction Littlehope Lane and Mordiford Road, Haugh Wood, Mordiford MF 1(2), SO 373578.

Paratype. GSM. PF 2837/1; Plate 2, fig. 5; same locality and horizon.

Description. The mean value of filament diameters (or the internal diameters of tubes) was found to be 6 μ for the Woolhope specimens but the only Wenlock Limestone



TEXT-FIG. 3. Comparative drawings of Silurian *Girvanella* all at magnification $\times 125$, showing the size and growth forms of the different species. (Opaque inclusions also indicated in *g*; tube diameter slightly above average in *d* and *i*.)

a, *G. fragila* sp. nov. *b*, *G. pusilla* sp. nov. *c*, *G. media* sp. nov. *d*, *G. proluxa* sp. nov. from Fownhope.
e, *G. problematica* Nich. and Eth. *f*, *G. problematica* var. *lumbricalis* Høeg. *g*, *G. sarmenta* sp. nov.
h, *G. incompta* sp. nov. *i*, *G. ramosa* sp. nov. *j*, *G. effusa* sp. nov.

specimen had a tube range of 2–4 μ . The tubes mainly have very dark grey granular calcite walls, 'algal dust' (Wood 1941). Branching may occasionally occur but is not readily visible.

Remarks. No processes of attachment were seen and as these forms were abundant in bedded limestones away from reef structures, it is possible that this species may have been a floating form. *G. fragila* and *G. pusilla* constitute the finest tubed Silurian species found. *G. fragila* can be distinguished readily from *G. pusilla* by its different growth habit, the latter being loosely coiled.

Distribution. This species has been found in the Woolhope Limestone around Mordiford where it is abundant at various horizons from just above the Petalocrinus Limestone to nearly the top of the Woolhope Limestone. It is extremely plentiful in the Scutterdine Quarries (Pocock 1930), sometimes appearing to be the dominant fossil in thin section. In the Wenlock Limestone the only specimen was found at Fownhope. No specimens were found in the limestones above this horizon.

Group PROBLEMATICA

Girvanella problematica Nicholson and Etheridge 1878

Plate 9, fig. 1; text-fig. 3e

Neotype. Figured by Wood (1957), Plate 5, fig. 2. Slide BM(NH) V34566. Stinchar Limestone, Ordovician, Tormitchell, Girvan, Ayrshire.

Description. Loosely coiling filament clusters with internal tube diameters 12–18 μ , occasionally more but mostly 15–16 μ , from the Silurian have been included in this species. This corresponds with Wood's redescription of the type species having average external tube diameters 21–22 μ ranging from 18 to 25 μ (rarely 30 μ) and internal diameter average 15–16 μ ranging from 13 to 20 μ (rarely 22 μ). *Girvanella* having adherent or tight branching or faggot-like groups are not here included. *G. problematica* has been found both as loose non-encrusting coils and encrusting brachiopods, crinoid ossicles, bryozoa, and tabulate corals.

Distribution. Woolhope, Wenlock Limestones, and the Bringewood Beds. This species is fairly common in the bedded Woolhope Limestone at Mordiford and a few specimens have been obtained from Old Radnor and Woolhope. It is fairly common to abundant in the Wenlock Limestone of Dudley, Fownhope, and Wenlock Edge, especially near Much Wenlock. It has been found also at May Hill, Ledbury, West Malverns, and Sollers' Hope, and is present in the Bringewood Beds (Aymestry Limestone) of Ledbury, View Edge (Craven Arms), and the Whitcliffe Beds, Ludlow.

Girvanella problematica var. *lumbricalis* Høeg

Plate 9, fig. 2; text-fig. 3f

1932 *Girvanella problematica* var. *lumbricalis* Høeg, pl. 1, fig. 6.

Description. Short strongly curving tubes, sometimes encrusting, but if so, only a small area of tube is in contact with the substrate (Pl. 9, fig. 2). Tubes non-adherent,

loosely interlaced or isolate, rarely branched, and do not taper. Diameter of the filaments varies from 12 to 18 μ , occasionally to 20 μ ; average diameter 14–17 μ .

Distribution. *G. problematica* var. *lumbricalis* has been found in the Wenlock Limestone of Dudley, Fownhope, and Wenlock Edge.

Girvanella pusilla sp. nov.

Plate 10, figs. 1–2; text-fig. 3b

Diagnosis. A loosely coiled *Girvanella* with fine thread-like tubes. Tubes long, even diameter, mostly unbranched, not usually in contact with each other except when encrusting other organisms. Diameter of tubes varies from 2 to 9 μ , very rarely to 11 μ , average 4–7 μ .

Holotype. GSM. PF 2838/2; Plate 10, fig. 1. Woolhope Limestone, Haugh Wood exposure, junction of Littlehope Lane and Mordiford Road, MF 1(2), SO 373578.

Remarks. Specimens obtained from the Woolhope Limestone were found to have a slightly larger tube diameter (mostly 5–7 μ), than those from the Wenlock Limestone (2–7 μ , mostly 4–5 μ). Specimens from the Wenlock Limestone of Fownhope and Dudley sometimes show filaments encrusting, sometimes with *Wetheredella*, different organisms including *Coenites* and crinoid ossicles. Filaments have also been seen in small growth forms in association with *Rothpletzella* and *Girvanella problematica*.

Distribution. *G. pusilla* occurs in the Woolhope and Wenlock Limestones of the Woolhope District; Woolhope, Mordiford, Fownhope, and Soller's Hope; the Woolhope Limestone of Old Radnor and the Wenlock Limestone of Wenlock Edge, Dudley, Ledbury, May Hill, and the west flank of the Malverns. This species was less abundant in the thin sections examined than *G. fragila* in the Woolhope Limestone, but more abundant in the Wenlock Limestone. Owing to the lack of clarity of most specimens for photographic purposes, the type specimen was selected from the Woolhope Limestone material.

Girvanella incompta sp. nov.

Plate 9, figs. 3, 4; Plate 10, fig. 1; Plate 11, fig. 1; text-fig. 3h

Diagnosis. Loosely coiled clusters of algal tubes. Tubes even diameter throughout and

EXPLANATION OF PLATE 9

Figs. 1, 2. DU 6, Wenlock Limestone. 1, *Girvanella problematica* Nich. and Eth., loosely coiled tubes, $\times 160$. GSM. PF 2842/1. 2, *G. problematica* var. *lumbricalis* Høeg, with short curving tubes encrusting trilobite pleura, $\times 160$. GSM. PF 2842/2.

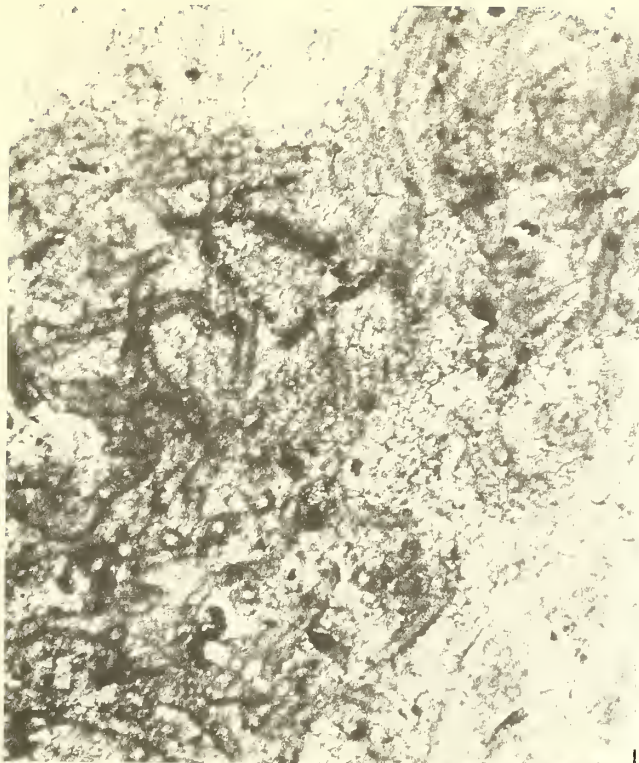
Figs. 3, 4. *G. incompta* sp. nov. WE 11, Wenlock Limestone. 3, Holotype; large loosely coiled tubes, some branching, $\times 140$. GSM. PF 2844/1. 4, Paratype; branching and curved tubes, $\times 250$. GSM. PF 2844/2.

EXPLANATION OF PLATE 10

Figs. 1, 2. *Girvanella pusilla* sp. nov. 1, Holotype; short coiling branched filaments; MF 1, Woolhope Limestone, GSM. PF 2838/2; $\times 250$. 2, Paratype; loosely encrusting specimen, $\times 250$; Woolhope Limestone MF 2(7); Author's coll.

Fig. 3. *G. media* sp. nov. Holotype; curved coiling, branched filaments; FH 2, Wenlock Limestone, GSM. PF 2840/1; $\times 145$.

Fig. 4. *G. incompta* sp. nov.; a few coiled tubes; WE 11, Wenlock Limestone, GSM. PF 2845/3; $\times 250$.



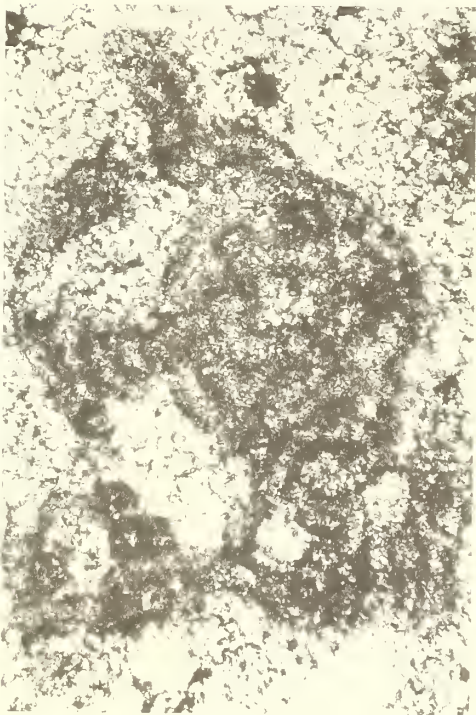
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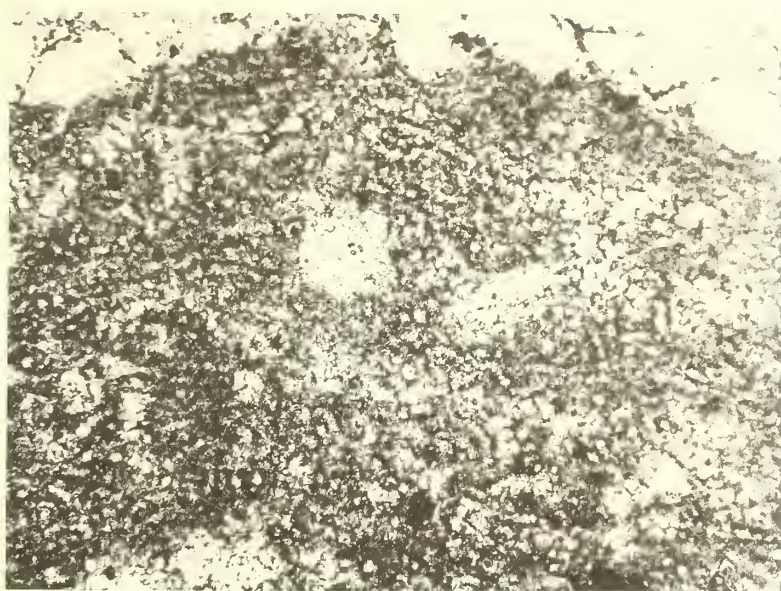
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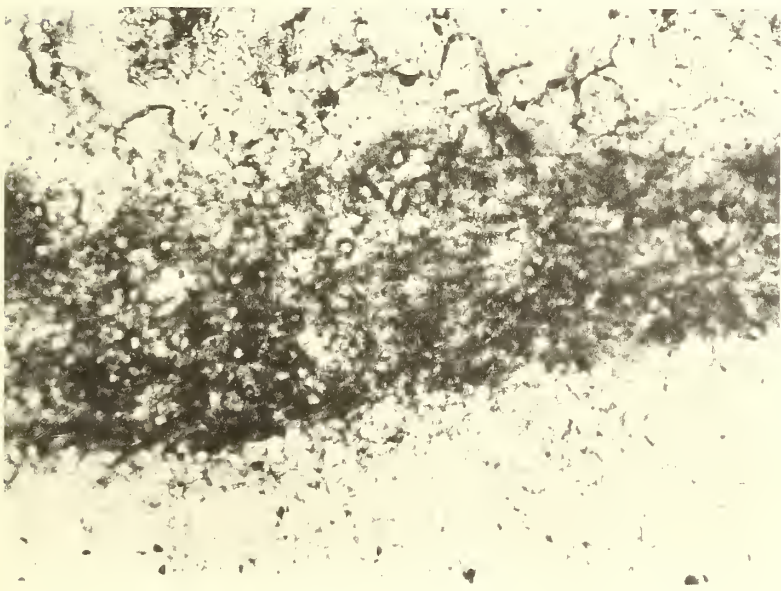
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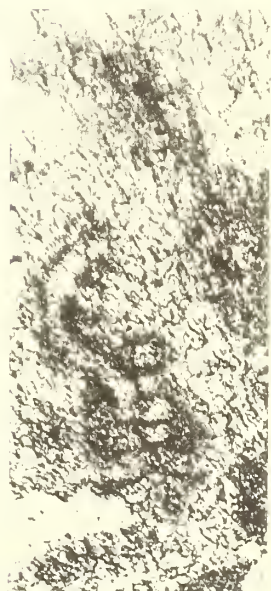
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usually branched. Tubes slightly to completely adherent with each other. Internal diameter of tube 18–28 μ , mostly 19–21 μ .

Holotype. GSM. PF 2844/1; Plate 9, fig. 3. Wenlock Limestone, Silurian. Wenlock Edge, WE 11(1), SO 844447.

Paratype. GSM. PF 2844/2; Plate 9, fig. 4. Same locality and horizon.

Description and Remarks. This species is variable in form. The variation extends from the typical very loose cluster of branching tubes to the occasional tight coiling of tubes or rarely one or two tubes arranged in a spiral form. The frequent occurrence of branching, the larger tube diameter, and the tendency of tubes to adhere to each other are the main features which separate this form from *G. problematica*. It has been found occasionally encrusting organisms such as brachiopods and bryozoa.

Distribution. Wenlock and Aymestry Limestones (Bringewood Beds). *G. incompta* was found to be abundant in the Wenlock Limestone at the south-west end of Wenlock Edge, but less common elsewhere. It also was found in thin sections taken from the Wenlock Limestone at Fownhope and Wren's Nest, Dudley and the Bringewood Beds of Aymestry Limestone of View Edge, Craven Arms.

Group MEDIA

Girvanella media sp. nov.

Plate 8, fig. 1; Plate 10, fig. 3; Plate 11, figs. 2–4; text-fig. 3c

Diagnosis. Tubes of even diameter adhering together, branching frequently and sometimes tightly coiled. Diameter range 8–18 μ , very rarely more, mostly 13–14 μ .

Holotype. GSM. PF 2840/1; Plate 10, fig. 3. Wenlock Limestone, Silurian. The Old Quarries, Common Hill, Fownhope FH 2(3), SO 348586.

Remarks. *G. media* differs from *G. problematica* in its adherent nature and frequent branching and from *G. incompta* by mode of branching and filament size. Occasionally it is found to have encrusted other organisms such as brachiopods and an ostracod.

Distribution. Woolhope, Wenlock, and Aymestry Limestones. *G. media* has been found at Woolhope and more at Mordiford (Woolhope Limestones). It occurs at Wenlock Edge, one specimen was found from Dudley but it is most abundant in the Wenlock Limestone at Fownhope. It has also been obtained from the Bringewood Beds (Aymestry Limestone) of View Edge, Craven Arms.

Group RAMOSA

Girvanella ramosa sp. nov.

Plate 12, figs. 1, 3, 5; text-fig. 3i

Diagnosis. Highly branched, uneven diameter tubes grouped together. Tubes are completely adherent to each other and branching is irregular. Diameters at internodes vary between 11 and 20 μ , average 15–16 μ .

Holotype. GSM. PF 2846/2; Plate 12, fig. 1. Wenlock Limestone, Silurian. Wenlock Edge WE 15(5), SO 856455.

Paratype. GSM. PF 2846/1; Plate 12, fig. 5. Same locality and horizon.

Description and Remarks. Most groups examined were small in size. The uneven diameter of the tubes of this species is due to the mode of branching and constrictions and in this they can be distinguished from the slightly smaller, branching even diameter tubes of *G. media*. In both this and the subsequent species *G. effusa*, the apparent constrictions might be related to either branching and/or cell length, if the original filaments were septate. No direct evidence has so far been found to support septation. Both these species are distinguished from *Rothpletzella* spp. by their irregular modes of branching and lack of the characteristic type of beading of a *Rothpletzella* (beading here representing cut branches).

Distribution. Woolhope and Wenlock Limestones. *G. ramosa* has been found in the Woolhope Limestone at Mordiford and the Wenlock Limestone of Fownhope and also Wenlock Edge where it is fairly common.

Girvanella effusa sp. nov.

Plate 12, figs. 2, 4; text-fig. 3j

Diagnosis. Tubes uneven in diameter, with some constrictions and highly branched. Branching is irregular and tubes are in contact with each other. Diameter of filaments at internodes 18 to 27 μ , mostly 22–23 μ wide.

Holotype. GSM. PF 2840/3; Plate 12, fig. 2. Wenlock Limestone, Silurian. The Old Quarries, Common Hill, Fownhope, Herefordshire, FH 2(3), SO 348586.

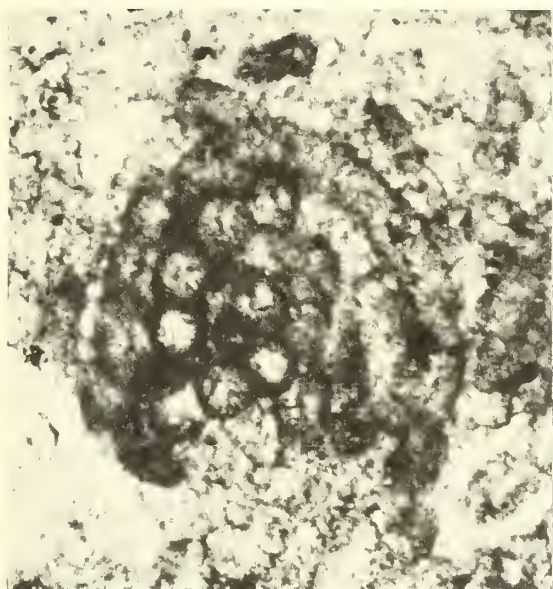
Description and Remarks. This species, like *G. ramosa*, has only short internodal lengths of filaments. The filaments curve and have a high branching frequency. The 'true' diameter is more difficult to find in this and the last species because of this high branching frequency, constrictions, and adhering tubes, so single measurements may read slightly lower than the limits shown for these forms. Graphs or histograms showing the range of diameters for each group are valuable and the 'peaks' on the graphs give better results than random measurements of odd filaments.

EXPLANATION OF PLATE 11

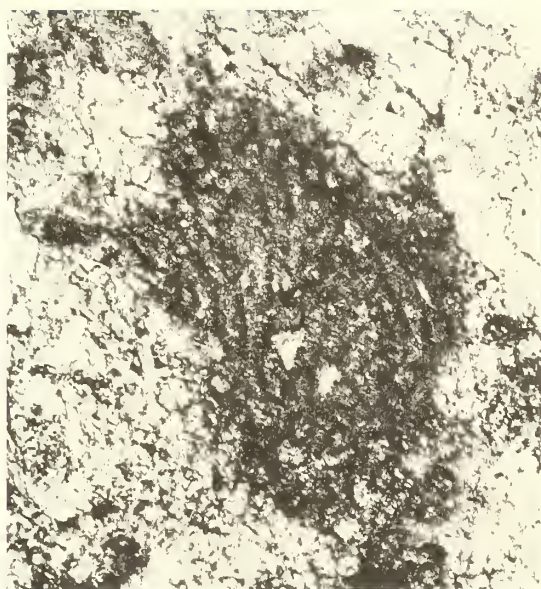
- Fig. 1. *Girvanella inconpta* sp. nov., coiled group. WE 11, Wenlock Limestone, GSM. PF 2844/3; $\times 270$.
Figs. 2–4. *G. media* sp. nov. 2, 3, branched specimens, tubes in contact; FH 2, Wenlock Limestone. 2, GSM. PF 2841/2; $\times 180$. 3, GSM. PF 2841/1; $\times 100$. 4, Less branched specimen, tubes short in length; MF 1, Woolhope Limestone, GSM. PF 2837/3, $\times 225$.

EXPLANATION OF PLATE 12

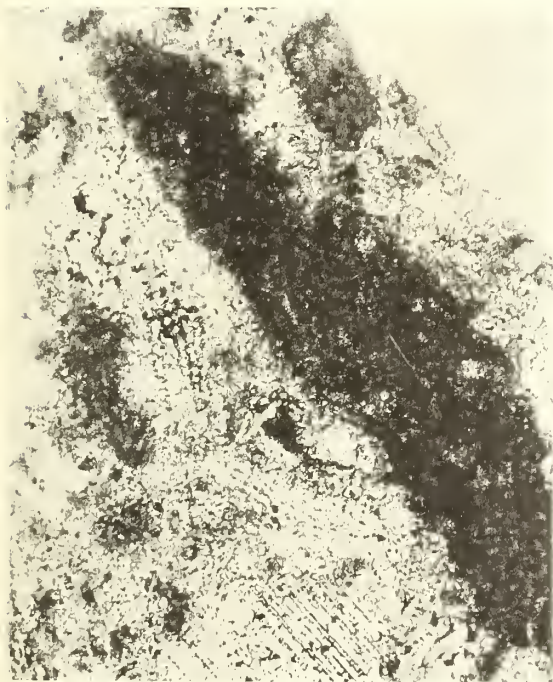
- Figs. 1, 3, 5. *Girvanella ramosa* sp. nov.; specimens with branched tubes of uneven diameter. 1, Holotype; WE 15, Wenlock Limestone, GSM. PF 2846/2; $\times 145$. 3, WE 11, Wenlock Limestone, GSM. PF 2844/4; $\times 180$. 5, Paratype; WE 15, Wenlock Limestone, GSM. PF 2846/1; $\times 145$.
Figs. 2, 4. *G. effusa* sp. nov. (larger diameter species than *G. ramosa*). 2, Holotype; FH 2, Wenlock Limestone, GSM. PF 2840/3; $\times 160$. 4, WE 11, Wenlock Limestone, GSM. PF 2845/1; $\times 160$.



1



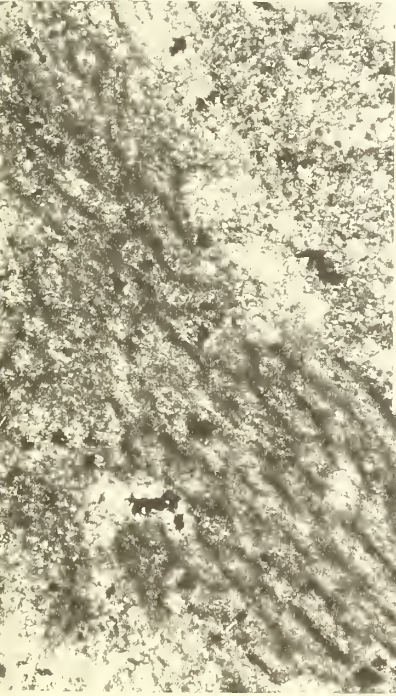
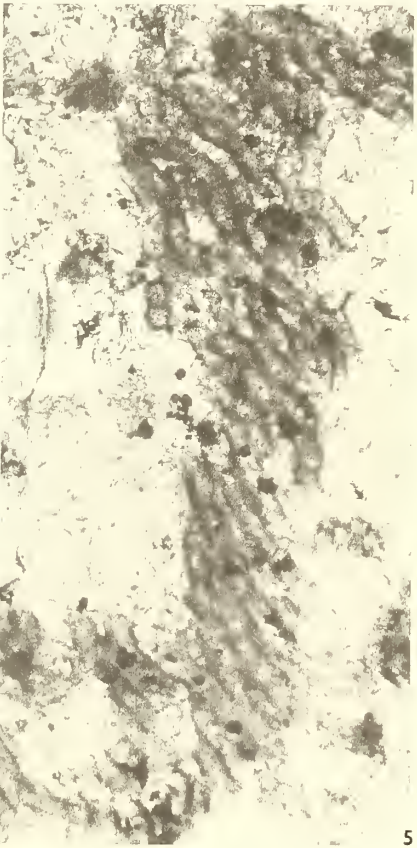
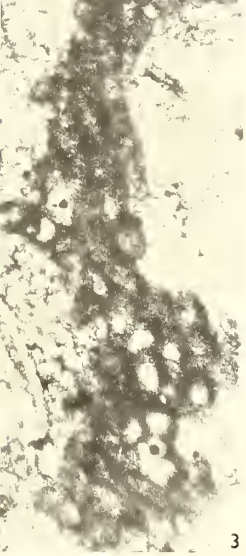
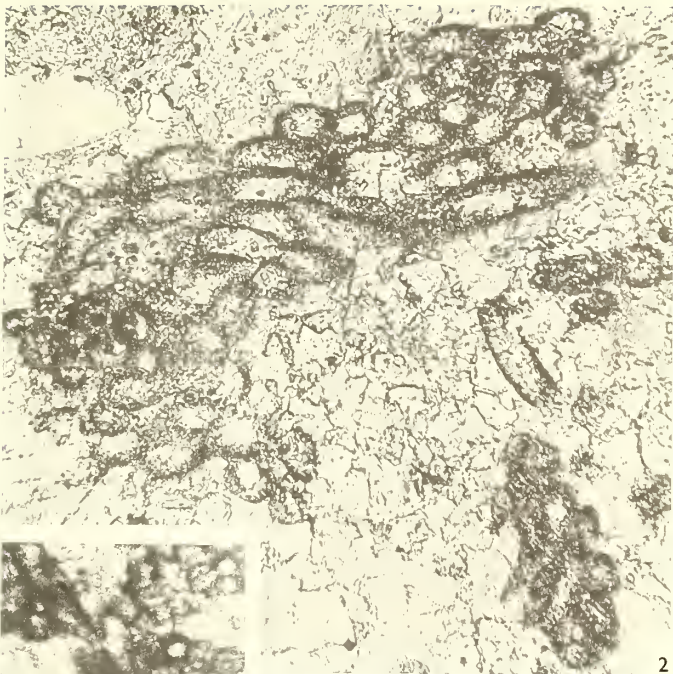
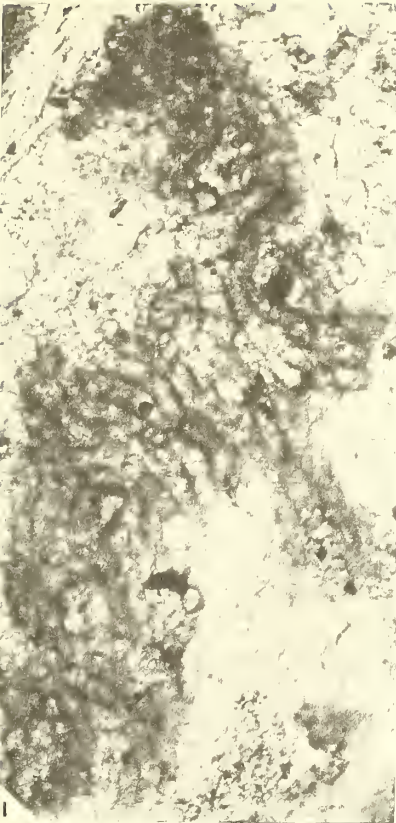
2



3



4



Distribution. Woolhope and Wenlock Limestones. Very few specimens have been obtained from the Woolhope Limestone (Mordiford). This species is found in the Wenlock Limestone at Fownhope and in the bedded sediments at Farley and south-western end of Wenlock Edge.

Acknowledgements. The author acknowledges assistance from many quarters during the progress of the work, in particular from Dr. F. W. Anderson, Dr. M. G. Calder, Professor P. W. Richards, and Professor P. W. Wardlaw. The final stages have been completed in the Durham University Geology Department thanks to the facilities kindly placed at my disposal by Professor K. C. Dunham; the plates have been prepared by Mr. C. Chaplin and Mr. G. Dresser, and text-figure 1 by Miss M. Lumley. A Durham University Research Fund grant towards the cost of preparing the paper is gratefully acknowledged.

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APPENDIX A

A Key to the Silurian species of *Girvanella*

1. Algal tubes less than 10 μ (rarely 11 μ) in internal diameter; tubes even in width.
 - (a) Tubes straight or slightly undulating; indefinite length with a moderate contact between adjoining tubes; arranged in bundles, diameters mostly 5–7 μ *G. fragila* (text-fig. 3a)
 - (b) Tubes short, of a finite length; branching variable; tubes in loose coils or encrusting, with adjoining tubes in contact; diameters 2–9 μ mostly between 4 and 7 μ *G. pusilla* (text-fig. 3b)
2. Algal tubes between 12 and 18 μ (rarely 20 μ).
 - (a) Tube diameter range (8) 12–18 μ , average 13–14 μ ; even in diameter.
 - (i) Tubes with frequent branching; adjoining tubes in contact; may or may not encrust; found in small groups *G. media* (text-fig. 3c)
 - (b) Tube with average diameter over 15 μ and under 18 μ ; even in diameter.
 - (i) Tube average diameter 15–16 μ ; long, slightly curved, with occasional branching; loosely coiling or meandering over a substrate; sometimes small amount of contact between tubes *G. problematica* (text-fig. 3e)
 - (ii) Tube average diameter 15–16 μ ; very short, many strongly curved; occasional contact between adjoining tubes. Found encrusting *G. problematica* var. *lumbricalis* (text-fig. 3f)
 - (iii) Tube average diameter 15–16 μ (in one locality recorded tubes average between 14 and 18 μ); indefinite length, straight or slightly undulating; adjoining tubes in contact and arranged in faggot-like bundles *G. prolixa* (text-fig. 3d)
 - (c) Tube diameter at internodes 11–18 μ (20 μ), average 15–16 μ ; diameter variable.
 - (i) Tubes irregular, curved; adjoining tubes in contact; branching frequent and possible constrictions *G. ramosa* (text-fig. 3i)
3. Algal tubes over 18 μ in diameter.
 - (a) Even diameter tubes in loose coils mostly not in close contact; branching occasional to frequent; non-encrusting; diameter range 18–28 μ , mostly 19–21 μ *G. incompta* (text-fig. 3h)
 - (b) Tubes even, long, straight or slightly undulating, arranged in bundles. Few tubes in close contact, branching rare; diameter range 18–31 μ , mostly 19–22 μ *G. sarmenta* (text-fig. 3g)
 - (c) Tubes large, uneven in diameter; branching frequent; also possible constrictions; adjoining tubes in contact; diameter at internodes 18–27 μ , mostly 22–23 μ *G. effusa* (text-fig. 3j)

APPENDIX B

List of *Girvanella* localities to which reference has been made in the text and plates.

Woolhope Limestone

1. Old Radnor, Radnorshire; Dolyhir Quarries and Yat Farm exposures (quarries *b*, *c*, *j*, *k*, Garwood and Goodyear 1918) OR 1+2, grid refs. SO 242582 and SO 246585.
2. Woolhope Village, Herefordshire; WH Exposure by road south of church, SO 357613.
3. Mordiford, Herefordshire; *a*, MF 1 Haugh Wood, several exposures; and junction with Littlehope Lane (beds just above *Petalocrinus* Limestone); SO 372578. *b*, MF 2 Scutterdine Quarries, Littlehope, SO 367581.

Wenlock Limestone

4. Wenlock Edge, Shropshire; WE 1-15, Various localities along its length from Farley; SO 015629 to SO 844447 and SO 856455 further south.
5. Dudley, Worcestershire; the Wren's Nest (DU), various exposures, SO 917935.
6. Fownhope, Herefordshire; FH, The Old Quarries, Common Hill, SO 348586.
7. Soller's Hope, Herefordshire; Lindell's Farm, SO 330522.
8. Woolhope area, Herefordshire; a small roadside exposure, SO 340622.
9. Longhope, Gloucestershire; Hobb's Quarry, SO 195695.
10. Ledbury, Herefordshire; Old Quarries by main Ledbury to Worcester road, SO 376715.
11. West Malverns; Disused quarry, Park Wood, SO 445763.

Bringewood Beds (Aymestry Limestone and the more calcareous Ludlovian facies)

12. View Edge, Craven Arms, Shropshire; SO 806426.
13. Ludlow, Whitcliffe; Old Quarry by River Teme, SO 742509.

LATE PERMIAN TRILOBITES FROM THE SALT RANGE, WEST PAKISTAN

by RICHARD E. GRANT

ABSTRACT. Three enrolled trilobites are the first reported from the Permian of the Salt Range. Two are assigned to *Ditomopyge fatmii* sp. nov., the third to *Kathwaia capitorosa* gen. et sp. nov. Correlations point to a Late Permian age (late Guadalupian or early Dzhulfian) making these among the youngest trilobites known.

FOSSILS have been known from the Productus Limestone of the Salt Range for more than 110 years. The first were collected in 1848 by Dr. A. Fleming, and described by Davidson (1862, p. 25). Since then the unusual abundance and excellent preservation of invertebrates in this region has attracted the attention of several palaeontologists who made large and detailed collections. The outstanding major work on invertebrates of the Productus Limestone is a series of monographs by W. Waagen, published between 1879 and 1891, based on collections made by Waagen and by several geologists of the Geological Survey of India. This was supplemented by several papers and a large monograph by Reed (1944), based on collections by Reed and others, especially E. R. Gee who spent several years mapping the geology of the Salt Range. Despite the extensive search for fossils in these strata, however, no trilobites were reported from the Productus Limestone. Waagen (1883, p. 402) does mention that 'trilobites' were reported from the Productus Limestone by Theobald, but that these turned out to be fragments of lepto- did brachiopods.

During the winter of 1963-4 the writer and A. N. Fatmi of the Geological Survey of Pakistan had the opportunity to collect fossils from the Productus Limestone, and were fortunate enough to find three well-preserved enrolled trilobites. These are described here because of the importance of the Productus Limestone fauna to the Permian of the world, and because their extreme rarity makes it unlikely that additional trilobite specimens will be available soon.

Acknowledgements. It is a pleasure to express appreciation to the Smithsonian Institution which, through G. A. Cooper, made possible the expedition to the Salt Range; to A. N. Fatmi, Geological Survey of Pakistan, who collected the two specimens of *Ditomopyge* described; to C. Teichert (now University of Kansas), M. G. White, and A. Davis (U.S. Geological Survey) all of whose help, both geological and logistical, made the stay in Pakistan most pleasant; and to C. Teichert and A. R. Palmer (U.S. Geological Survey) for criticism of the manuscript. The photographs are by D. H. Massie, and the text-figure is by E. Stromberg (U.S. Geological Survey). This publication is authorized by the Director, U.S. Geological Survey.

Stratigraphy of the Productus Limestone. The Productus Limestone is composed of three units, traditionally designated the Lower, Middle, and Upper Productus Limestones. Teichert (in press) has recognized that these are palaeontological units as currently defined, following usage by Waagen (1889) and subsequent workers. However, they also approximate the actual lithic breakdown of the Productus Limestone, and, in fact, have been mapped as rock units by E. R. Gee (unpublished data).

The Lower Productus Limestone (i.e. the lower lithostratigraphic unit) is 200–500 ft. thick, mostly sandstone, with the proportion of calcareous cement increasing upward. Near the top it is sandy or silty, and in places argillaceous. It contains fusulinids, predominantly *Parafusulina kattaensis* (Schwager), in the lower three-fourths; these forms are especially abundant in two rusty brown calcareous sandstone ledges that normally occur about 40–80 ft. below the top. These fusulinids are considered by Dunbar (1933) and Dunbar *et al.* (1960) to be Artinskian in age, near the middle of the Lower Permian of the present classification (Sarycheva, ed. 1960, p. 10; Cohee 1960, p. 1578; Dunbar *et al.* 1960).

The Middle Productus Limestone is the only unit of the group that actually is predominantly limestone. It is a thick-bedded biosparite that forms a prominent cliff ranging from about 200 ft. to more than 500 ft. in height. The lower beds are somewhat clayey or silty, with bedding planes 3–6 ins. apart; the middle beds are much thicker, up to 5 or 6 ft.; the upper beds of the cliff-forming limestone are thinner, like those near the base. At the top of the cliff a very fossiliferous unit of shaly limestone and calcareous shale or siltstone that normally weathers back from the cliff into irregular nodular beds is included in the Middle Productus Limestone.

Above the nodular beds are about 40 ft. of weakly resistant green shale, or less commonly fine-grained sandstone, forming the base of the Upper Productus Limestone. This is followed by beds of sandstone, varying in grain size, amount of calcareous cement, and abundance of fossils, which bring the aggregate thickness of the Upper Productus Limestone to about 200 ft. The ammonoid *Cyclolobus* occurs in the upper third of this unit, indicating a Late Permian (Dzhulfian) age (Glenister and Furnish 1961, p. 684).

Occurrence and age of the trilobites. All three specimens are from the uppermost beds of the Middle Productus Limestone, weathered out of the unit of alternating calcareous shale and nodular argillaceous limestone. This upper unit is 43 ft. thick at Zaluch Nala where *Ditomopyge* was found (fig. 1, loc. 2) and 23 ft. thick in the vicinity of Kathwai where *Kathwaia* was collected (fig. 1, loc. 1).

The uppermost beds of the Middle Productus Limestone are faunally similar to the Upper Productus Limestone, and faunally distinct from the Lower Productus Limestone (for faunal lists see Waagen 1889, pp. 180–242). Therefore the trilobites can be considered late Guadalupian or early Dzhulfian, depending upon the range of *Cyclolobus* and the significance attached to the faunal similarity of the uppermost Middle and the Upper Productus Limestone. If this assignment is correct, the Salt Range trilobites are among the latest known (Harrington *et al.* 1959, pp. O 399–O 403).

Two fragmentary pygidia from the Chitichun Limestone of Tibet (Diener, 1897, pp. 3–6) were found with brachiopods that closely resemble many from the top of the Middle Productus Limestone, and therefore may be the same age as the Salt Range trilobites. However, Diener (1903) found the ammonoid *Cyclolobus* in the same unit as his trilobites, which suggests that they may be slightly younger than the Salt Range specimens.

Classification. Meaningful classification of the few genera of Permian trilobites necessarily depends upon correct understanding of the systematic affinities of their Carboniferous forebears. Hessler (1963, p. 543) has undertaken such a study in conjunction with his work on Mississippian Proetidae, and has indicated that he will offer a classification

of this group in a forthcoming paper. Therefore, no suprageneric breakdown of proetids or phillipsiids is attempted here.

Genus DITOMOPYGE Newell 1931

1931 *Ditomopyge* Newell, p. 267, emend. 1935, Weller, J. M., p. 505.

1933 *Cyphinium* Weber, pp. 45, 81.

1937 *Neophillipsia* Gheyselinck, p. 56.

Type species. *D. lansingensis* Newell 1931, p. 268, pl. 31, figs. 31–32.

Diagnosis. *Cephalon* subtrigonal in outline, genal spines short. Glabella anteriorly expanding, but not strongly inflated; three preoccipital lobes at posterior. Eyes prominent, reniform, not elongate, located beside posterior third of glabella. *Thorax* with nine segments. *Pygidium* nearly the same as cephalon in size and outline. Axis with 12–18 segments, pleural regions with somewhat fewer. Border distinct but without border furrow; flat or concave, downsloping. *Ornamentation* weak, consisting of striations on cephalic border and underside of pygidial border, and a transverse row of low pustules or slightly elongated tubercles on each axial ring. Other ornamentation, such as low granules or shallow pits on cephalon, may be present.

Discussion. The generic position of *Cyphinium* Weber has been discussed fully by Weller (1935, p. 504; 1936, p. 711); it is to be regarded as a junior synonym of *Ditomopyge*.

The genus *Neophillipsia* Gheyselinck was established on a supposedly Upper Carboniferous specimen from Kansas, and Weller (1944, p. 320, pl. 49, fig. 3) demonstrated beyond doubt that it belongs to *Ditomopyge*. In addition, he offered convincing evidence that it was collected from beds in southern Kansas that now are considered to be Lower Permian.

Mudge and Yochelson (1962, p. 96) report a specimen from the Lower Permian of Kansas which they identify as *Ditomopyge? decurtata* (Gheyselinck). Their specimen was collected from slightly higher in the section than where Weller surmised Gheyselinck's was obtained. They mention that the border continues around the anterior of the glabella and thus differs from Weller's (1936, p. 711) diagnosis. The Salt Range specimens also differ in this feature, and perhaps are more closely related to the stratigraphically slightly higher form described by Mudge and Yochelson; other characters resemble closely those of *D. scitula* (Meek and Worthen) and *D. decurtata* (see Pl. 13, figs. 4, 5).

Comparisons. Only *Pseudophillipsia* Gemmellaro (1890, p. 14) resembles *Ditomopyge* sufficiently to warrant comparison here. To judge from reconstructions of *Pseudophillipsia* by Gemmellaro (1890, pl. 2, fig. 4) and Weller (1944, pl. 49, fig. 10; also in Harrington *et al.* 1959, fig. 307, no. 4) and a systematic analysis by Goldring (1957), it differs from *Ditomopyge* in its more anteriorly divergent facial sutures, smaller and sharper basal pre-occipital lobes, strong granular ornamentation of the posterior of the glabella, and its great number of pygidial segments.

Presence of a distinct cephalic border on the Salt Range species, and the Kansas Permian specimens called *Ditomopyge? decurtata* by Mudge and Yochelson (1962) may be another indication of the close relationship of *Ditomopyge* with *Pseudophillipsia* that was emphasized by Goldring (1957, pp. 197 *et seq.*). Goldring suggested that *Ditomopyge* as now constituted may involve two subgenera, one with a border, presumably

more closely related to *Pseudophillipsia*, and one lacking a border. *Ditomopyge* is distinguished from *Pseudophillipsia* by other features, important among which is its smaller number of pygidial segments (Goldring 1957, p. 199).

Ditomopyge fatmii sp. nov.

Plate 13, figs. 2a-d, 3

Diagnosis. Cephalon with distinct border, slightly raised to form short flange; shallow border furrow continuing around anterior of cranidium; genal spines short; pygidium with seventeen axial segments and broad border.

Description. Carapace essentially smooth, ornamented only by few granules on posterior part of glabella, weak striations on cephalic border and underside of pygidial border, and by transverse row of low sagittally elongate tubercles on crest of each axial ring of thorax and pygidium. Cephalon subtrigonal in outline, somewhat flattened on top, then sloping steeply toward border, thus producing strong curvature of anterior end of glabella, and of librigenae. Glabella elongate, anteriorly expanding but not inflated, with three distinct pre-occipital lobes; lateral pair slightly longer than median one. Glabellar furrows other than those outlining pre-occipital lobes, absent. Occipital ring without median tubercle. Palpebral lobes small, crescentic, located posterior to mid-length of glabella. Facial sutures strongly divergent anterior to eyes, then convergent across border; posterior course cutting diagonally postero-laterally across posterior border. Eyes prominent, outline nearly semicircular, not elongate. Librigenae trapezoidal, posterior border furrow flexed posteriorly, distal edge of cheek produced to form short genal spine. Thorax composed of nine segments; distal ends of pleurae bent gently downward. Pygidium proportionately large: size and outline conforming to that of cephalon. Axis with seventeen segments and terminal axial piece, crest flattened and nodular; pleural regions with twelve slightly sigmoidal segments; interpleural furrows shallow, pleural furrows indistinct. Border distinct, rather broad, gently concave, without border furrow.

Measurements (in mm.)

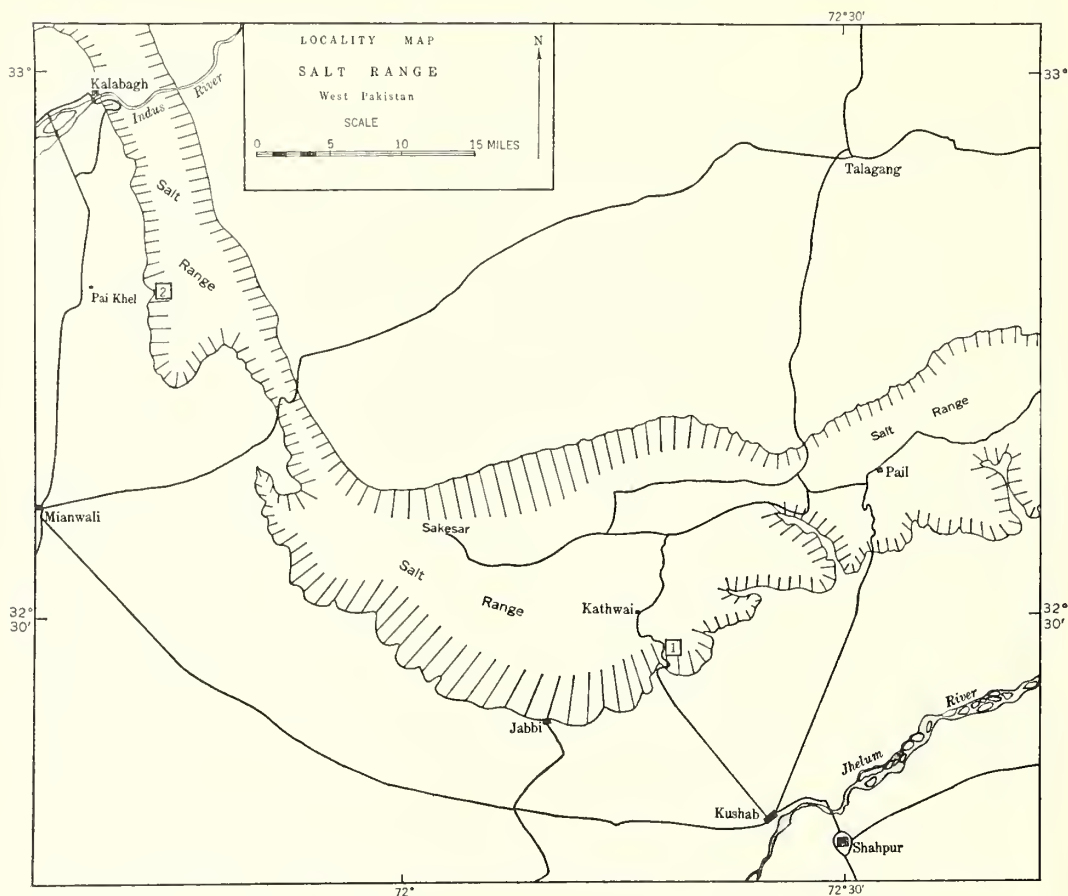
	<i>Cephalon</i>		<i>Thorax</i>		<i>Pygidium</i>	
	<i>Length</i>	<i>Width</i>	<i>Length</i>	<i>Width</i>	<i>Length</i>	<i>Width</i>
Holotype, G.S.P.B. no. 88 Plate 13, figs. 2a-d	8·8	11·5	10·8	10·2	8·8	10·7
Paratype, G.S.P.B. no. 89 Plate 13, fig. 3	7·9	c. 10		9·5		

Locality. Both specimens were collected from the Middle Productus Limestone, on the divide between Kala Wahan and Zaluch Nala, east of Pai Khel, Survey of Pakistan map 38 P/9 (text-fig. 1, loc. 2). These beds can be traced along this divide between the two valleys, about one mile upstream from their mouths. The holotype was found nearer Zaluch Nala, and the paratype nearer Kala Wahan.

Repository. The specimens are deposited in the collections of the Geological Survey of Pakistan, where they have been assigned catalogue numbers G.S.P.B. 88 and 89.

Comparisons. *Ditomopyge fatmii* differs from *D. scitula* (Meek and Worthen) in its more distinct cephalic border marked by a border furrow that continues around the

anterior of the glabella, its smaller eyes which are distinctly less than half as long as the glabella, its greater number of pygidial segments, and probably also in its much shorter genal spines. The spines are broken from both of the available specimens, but the shape of the librigenae and the posteriorly directed course of the posterior border furrow are



TEXT-FIG. 1. Map of part of Salt Range, showing localities from which trilobites were obtained.

similar to those of *D. decurtata* (Gheyselinck), which has only short genal spines (Pl. 13, figs. 4, 5). The Salt Range species differs from *D. decurtata* in its complete cephalic border and border furrow, somewhat greater number of pygidial segments, and its wider and more concave pygidial border.

Ditomopyge meridionalis Teichert (1944, p. 458) was described from the Wandagee Formation of Western Australia, considered to be of Artinskian age (Teichert 1944, p. 456; Glenister and Furnish 1961, p. 679). This species differs from *D. fatmii* in its proportionately shorter and more bulbous glabella, less prominent pre-occipital lobes, and by the much smaller number of axial and pleural segments on the pygidium. In addition Teichert (1944, p. 460) remarks on the unusual length, for a Permian species, of the genal spines of *D. meridionalis*.

Among Lower Carboniferous species described by Weber (1933) none seem closely similar to *D. fatmii*. The cephalic border of *D. acanthicaudum* (Weber) is very narrow, according to Weber (1933, p. 84), and the pygidium has somewhat fewer axial and pleural segments. The eyes seem to be proportionately larger than in *D. fatmii*, and the pre-occipital lobe more prominent. *Ditomopyge kumpani* (Weber) is ornamented by conspicuous granules, and although the variety *crassicrusta* appears smooth, Weber (1933, p. 85) says that it is exfoliated.

The Artinskian species *D. artinskiense* (Weber) differs from *D. fatmii* in its more anteriorly expanding glabella, distinctly fewer pygidial segments, and more or less transverse, rather than subcircular, median pre-occipital lobe. According to Weber (1933, p. 89) the genal spines extended posteriorly nearly to the pygidium, much further than in *D. fatmii*, and more like the Australian species *D. meridionalis* Teichert. The trend toward decreasing length of genal spines in stratigraphically younger species of *Ditomopyge* has been noted by Weller (1937, p. 346, text-fig. 4). The short spines of *D. fatmii* argue further for its Late Permian age.

Genus KATHWAIA gen. nov.

Type species. Kathwaia capitorosa sp. nov.

Diagnosis. Cephalon semicircular in outline, genal spines absent. Glabella inflated, protruding anterior to border, with two small but prominent lateral pre-occipital lobes. Eyes small, near mid-length of cephalon. Thorax with nine segments. Pygidium short, with border but no border furrow. Ornamentation granular, present on all parts but strongest on cephalon.

Description. The genus is monospecific at present; therefore its characters are given below in the description of the type species.

Couparisons. This genus shares features with several genera of phillipsioid trilobites. It resembles *Phillipsia* Portlock in its general shape, granular ornamentation, and indistinctly delimited pygidial border. It differs from that Lower Carboniferous genus in its lack of genal spines, its non-continuous cephalic border, smaller eyes located farther anterior, absence of glabellar furrows (other than those outlining pre-occipital lobes) and in its fewer pygidial segments. It is similar to *Griffithides* Portlock in its granular ornament and lack of genal spines, but differs in its swollen glabella, non-continuous cephalic border, semicircular rather than semi-oval or subtrigonal outline of the cephalon, more prominent lateral pre-occipital lobes, and fewer pygidial segments. Despite the Early Carboniferous age of *Griffithides*, it is the genus most similar to *Kathwaia*.

Humiligriffithoides Inai, recently discussed by Endo and Matsumoto (1962, p. 159), resembles *Kathwaia* in its swollen glabella and lack of genal spines. It differs from the Salt Range genus in its smooth carapace, sharp genal angle, larger eyes, short lateral glabellar furrows, and its well-defined pygidial border.

Among Permian genera only *Neoproetus* Tesch resembles *Kathwaia* in more than general aspect. The glabella of *Neoproetus* is bulbous and overhangs the anterior margin as in *Kathwaia*, similarly the ornamentation of the cephalon is granular, although *Neoproetus* also has some wrinkles on the anterior part of the glabella (Weller 1944, p. 325).

Kathwaia differs from *Neoproetus* in its semicircular rather than subtrigonal cephalon, its proportionately longer glabella, more inflated lateral pre-occipital lobes, smaller eyes, more rounded genal angle, divergent anterior course of the facial sutures, and in the granular ornamentation that is present over the whole carapace, not confined to the cephalon as in *Neoproetus*. The number of pygidial axial segments is 9 or 10 in both species of *Neoproetus*, *N. indicus* Tesch and *N. verrucosus* (Gemmellaro); it is 8 on the one known specimen of *Kathwaia*. In addition, the pygidium of *Neoproetus* is described by Gheyselinck (1937, p. 76) and Weller (1944, p. 325) as having a slightly segmented or crenulated border. This feature is not present in *Kathwaia*.

The Middle Permian genus *Paraphillipsia* Toumansky (1935) from the Crimea and Himalaya differs from *Kathwaia* in its broader glabella, wider and more inflated pre-occipital lobes, small eyes, and its proportionately short pygidium with laterally short pleurae and very broad, granular, convex border.

Other Permian genera such as *Pseudophillipsia* Gemmellaro, *Ameura* Weller, and *Anisopyge* Girty seem to belong to the group of trilobites containing *Ditomopyge*, and do not strongly resemble *Kathwaia* or *Neoproetus*. *Neogriffithides* Toumansky from the Permian of the Crimea has rounded genal angles similar to those of *Kathwaia*, although according to Weller (1944, p. 326) these were reconstructed from disassociated librigenae, and may not belong to *Neogriffithides*. This doubt is reflected by Weller in his reconstruction of that genus in the *Treatise on Invertebrate Paleontology* (Harrington *et al.* 1959, fig. 306, no. 6). The multi-segmented pygidium of *Neogriffithides*, with its flattened distinct border, is the chief distinction from *Kathwaia*.

Additional species. The granular species *Proetus? girtyi* Toumansky, from Crimean rocks considered by Toumansky (1935, p. 38) to be Guadalupian in age, may belong to *Kathwaia*. It differs rather strongly from the type species, *K. capitorosa*, in features that may be considered generic. It has a proportionately broader axis, 10 rather than 9 thoracic segments, stronger granular ornament, and differs markedly by possession of a cephalic

EXPLANATION OF PLATE 13

All figures $\times 3$.

Figs. 1a-d, *Kathwaia capitorosa* gen. et sp. nov., enrolled holotype from upper part of Middle Productus Limestone, south of Kathwai (text-fig. 1, loc. 1), USNM 145320. a, dorsal view of cephalon and part of thorax; b, dorsal view of pygidium and part of thorax; c, left lateral view of enrolled specimen; d, anterior view.

Figs. 2a-d, *Ditomopyge fatmii* sp. nov., enrolled holotype from upper part of Middle Productus Limestone at Zaluch Nala (text-fig. 1, loc. 2). GSPB 88. a, dorsal view of cephalon and part of thorax; b, dorsal view of pygidium and part of thorax; c, right lateral view of enrolled specimen; d, anterior view.

Fig. 3, *D. fatmii* sp. nov., incomplete enrolled paratype from locality 2 (text-fig. 1), GSPB 89. Dorsal view of cephalon and part of thorax.

Figs. 4a-c, *Ditomopyge decurtata* (Gheyselinck), enrolled topotype from Permian Beattie Limestone near Wichita, Kansas, for comparison with *D. fatmii*, USNM no. 145322. a, dorsal view of cephalon and part of thorax; b, dorsal view of pygidium and part of thorax; c, left lateral view of enrolled specimen.

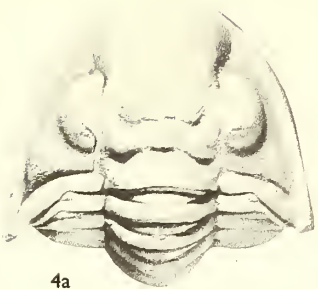
Figs. 5a-b, *D. decurtata* (Gheyselinck), enrolled specimen from Florena Shale Member of Beattie Limestone, East of Grand Summit, Kansas, for comparison with *D. fatmii*, USNM no. 145321; a, dorsal view of cephalon and part of thorax; b, dorsal view of pygidium and part of thorax.



1a



2a



4a



1b



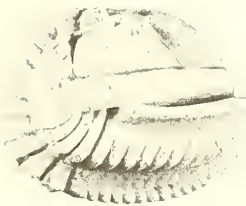
2b



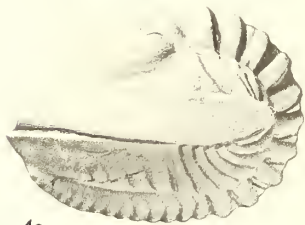
4b



1c



2c



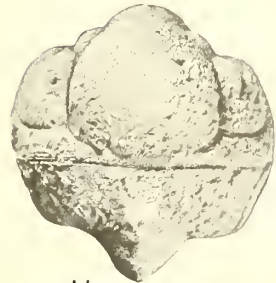
4c



2d



5a



1d



3



5b

border, which is said to be longitudinally striated. Aside from this possible additional species, no species other than the type is known to belong to *Kathwaia*.

Kathwaia capitorosa sp. nov.

Plate 13, figs. 1a-d

Diagnosis. Glabella strongly inflated, projecting anteriorly beyond cephalic border. Occipital ring rather broad sagittally, with small median node. Pygidium with eight axial segments plus terminal piece, length about two-thirds that of cephalon, border flat to slightly convex, broad but indistinctly delimited from pleural areas, lacking border furrow.

Description. *Carapace* with relatively strong granules randomly and rather densely distributed on cephalon, and in apparent rows on axial rings; weaker granules on pleural regions of thorax and pygidium. Edge of border to cephalon and pygidium weakly striated. *Cephalon* approximately semicircular in outline, strongly convex. Glabella (exclusive of lateral preoccipital lobes) strongly inflated to tear-drop shape, extending anteriorly beyond border, interrupting anterior course of border except at very margin. Lateral pre-occipital lobes proportionately large, inflated, each subtrigonal in outline. Eyes small, hemispherical (not elongate); midlines located at furrows marking anterior ends of lateral pre-occipital lobes, about midlength of cephalon (exclusive of anterior glabellar protrusion). Facial sutures nearly parallel to axis between eyes and posterior border furrow, then strongly divergent posteriorly across border; anterior course moderately divergent anterior to eyes, then convergent around glabella. *Librigenae* strongly convex laterally; sides nearly vertical; genal angle gently and evenly curved, without genal spines. Occipital ring somewhat constricted laterally by posterior edges of lateral pre-occipital lobes; low node on crest. *Thorax* with 9 segments; pleural segments strongly flexed and sloping steeply to lateral margins. *Pygidium* about two-thirds actual length of cephalon (excluding protrusion of glabella). Axis with 8 rings and terminal axial piece; pleural regions with 7 pleurae, each subdivided by shallow furrow increasing in depth laterally. Border broad, border furrow absent, proximal edge marked only by terminations of pleural and inter-pleural furrows. Margin weakly striated, outline conforming exactly to that of cephalon, forming tight seal during enrolment.

Measurements (in mm.)

	Cephalon		Thorax		Pygidium	
	Length	Width	Length	Width	Length	Width
Holotype, USNM no. 145320	8.5	12.0	16.7	12.0	6.5	10.7
Length of cephalon including protruding glabella	9.0					

Locality. *Kathwaia capitorosa* was collected from beds at the top of the cliff of Middle Productus Limestone, 5.5 miles road-distance south of Kathwai, on the road to Kushab, Survey of Pakistan map 43 D/3 (fig. 1, loc. 1). The Middle Productus Limestone is faulted in such a manner that part of the cliff and the uppermost beds are repeated three times. The road passes over the lowermost fault block; the trilobite was collected from the uppermost one, two fault 'steps' above the east side of the road, about 250 ft. above road level.

Discussion. With only one specimen available, it is uncertain which characters are diagnostic of the species. The diagnosis was composed with reference to species of the seemingly most nearly related genus, *Neoproetus*, with the assumption that species characters in *Kathwaia* are analogous.

Repository. The specimen is deposited in the United States National Museum.

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THE MICROSTRUCTURE OF STROMATOPOROIDS

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ABSTRACT. Fourteen microstructures are recognized in stromatoporoid tissue, but not all are features of the tissue laid down by the organism and much fibrous, transversely porous, flocculent, pseudotubular, and melanospheric tissue has developed from other microstructures during the process of preservation. Irregular specks of opaque matter less than $5\ \mu$ across are present in the tissue of most stromatoporoids but some have uniformly coloured tissue. During preservation these specks have moved, diffusing out into the galleries and concentrating into spheres. Fibrosity caused by intercrystalline boundaries and by the alignment of the specks transverse to the structural elements or in a water jet pattern is both an original microstructure and developed during preservation. Compact tissue in which the specks are evenly distributed passes through stages of alteration due to the concretionary tendency of the specks, in which it is successively flocculent, pseudotubular, and finally characterized by dark spherules (melanospheres).

Tissue of the family Stromatoporidae is marked by subspherical voids or dark spherules. Originally the tissue was cellular, filled with subspherical voids. The tissue marked by dark spherules is here called melanospheric tissue and has been altered by the breakdown of the walls between the cellules and the concentration of the dark specks in the regions between. A puzzling feature is the occurrence of other microstructures such as microlaminae, tubules, tripartite laminae, etc., in both black-on-white and white-on-black states interchangeably.

The microstructures of 22 common genera and of the family Labechiidae are reviewed and emended diagnoses of genera provided. *Clathrodictyon* cannot be defined in terms of cysts placed side to side, as the holotype has regular continuous laminae. The laminae of *Stictostroma* and *Stromatoporella* contain a single line of cellules opening to the galleries on either side by a pore. *Clathrocoilonia* has compact tissue and is closely allied to *Stictostroma*. *Actinodictyon* and *Pseudoactinodictyon* have compact tissue and are similar to *Clathrodictyon* and *Anostylostroma* respectively. *Trupetostroma* has vacuolate tissue but the vacuoles are not concentrated at the peripheries of the pillars. The median light zone of its laminae is probably the result of the merging of a plane of cellules during preservation. Most species of *Idiostroma* should be assigned to other genera as they have in common little but external form and do not have the microstructure of the type species. *Hermatostroma* is polyphyletic and includes species with compact and cellular tissue. It is characterized by marginally cellular or vesicular pillars. The tissue of *Stachyodes* contains fine dark or light rods. *Parallelopora* may be distinguished from other members of the family Stromatoporidae by its large cellules arranged in vertical series. The cysts of the Labechiidae are a single thin layer of compact tissue and the enclosing layers of flocculent or striated tissue are due to diffusion of specks into the galleries during preservation.

PALAEONTOLOGISTS of the early and middle parts of the nineteenth century described stromatoporoids in terms of their external form and surface. Rosen (1867), Nicholson (1886–92), and others discovered the internal structure of these fossils by examining them in thin sections cut tangentially and perpendicular to the banding. The coenosteum was revealed as composed mainly of laminae, pillars, cysts (or dissepiments), and amalgamate tissue in various combinations. These, and a few others that occur rarely, may be referred to as the *structural elements* of the stromatoporoid coenosteum and their arrangement defines a *structure*. Nicholson showed that the stromatoporoids could be divided into species, genera, and families on the basis of their structure. He also described the *microstructures* of the tissue which is the substance of the structural elements and distinguished non-porous, porous, and tubulated tissue. Heinrich (1914) based a classification of the stromatoporoids on the microstructure of the tissue and since that time students of this group have taken various stands on the nature of the microstructures of various genera, the significance of microstructures for classification, and the extent to which different microstructures are the result of the processes of preservation. In one of the two recently published classifications (Galloway 1957) the

microstructure of the tissue is important in separating families and genera; in the other (Lecompte 1951-2) differences in microstructure are considered to be largely secondary.

The lack of agreement on the interpretation of the microstructure of the order is well illustrated by a review of opinions on the tissue of the genus *Stromatopora* and the family Stromatoporoidae. The tissue of the genus occurs in two states: either marked by light dots on a darker background or by dark dots on a lighter background. Nicholson (1886-92) described the tissue as porous and recognized the light dots as vacuities that may be filled with bituminous matter in some states of preservation so that they appear to be darker than the surrounding tissue. His concept of the nature of the tissue is better expressed by the term cellular. Parks (1936) did not consider the Stromatoporidae extensively but believed that their structure was like that of *Actinostroma* on a much smaller scale; that is, the light tissue contained an open, three-dimensional lattice of dark tissue. Yavorsky, in his extensive writings on this group, well summarized in 1963, followed Nicholson in describing the tissues as porous. Lecompte (1951-2, 1956) described the tissue as 'cellulaire' or 'alveolaire' with the cells arranged in a reticulate pattern. He believed that the fundamental microstructure of stromatoporoids whose tissue others would describe as maculate, vacuolate, porous, or striated is microreticulate. He also believed that the study of microstructures is not far enough advanced to provide a basis for classification.

Against the writers noted above Galloway (1957), and Galloway and St. Jean (1957) maintained that the microstructure of *Stromatopora* is not porous or cellular. They described it as marked by maculae which are typically dark dots with a light centre but may appear as solid dark or light dots. They would also distinguish other types of microstructure in the stromatoporoids, such as microreticulate, porous, vacuolate, etc., which are not accepted as distinct from cellular by Lecompte. St. Jean (1963) has recently reviewed the concept of maculate microstructure.

Such opposing views require reconciliation before a classification can be based on the microstructure of this group. Such a reconciliation is attempted in this paper but no new classification is presented.

Faced with difficulty in applying the schemes of classification based on microstructure to the determination of stromatoporoids from western Canada, I tried to seek the basis for the conflicts by studying the major collections during 1964. Those examined were: parts of the Galloway and St. Jean collection at the University of North Carolina; the Nicholson collection at the British Museum (Natural History); the type materials of Bargatzky, Maurer, and Heinrich, assembled by E. Flügel, at the Technische Hochschule, Darmstadt; the Ripper collections of Australian stromatoporoids at the British Museum and at the Sedgwick Museum, Cambridge; and type specimens of Parks's genera at the Royal Ontario Museum, Toronto. Unfortunately the collections of Lecompte at Brussels were unavailable for study.

The Mesozoic sphaeractinoids were not considered as stromatoporoids for the purposes of this paper and their structure was reviewed by examination of the Hudson collection at the British Museum (Natural History) only for purposes of comparison.

Thin sections in the Nicholson collection at the British Museum (Natural History) are referred to by Nicholson's number with the prefix 'Nich.'. Thin sections at the University of North Carolina are referred to with the prefix UNC and those at the Royal Ontario Museum with the prefix ROM.

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CLASSIFICATION OF MICROSTRUCTURES

The Scale of Microstructures. The structural elements are composed of tissue that is commonly several hundreds of microns thick (wide as it appears in thin section). To see microstructures which have dimensions in the range 0.5–50 μ this tissue must be examined in suitably thin sections at magnifications of 50–100 times. Photographs at magnifications less than 20 times do not show microstructures clearly. Very few papers describing stromatoporoids present photographs of magnifications suitable for the study of microstructures (exceptions are St. Jean 1960, 1962). In thick sections which may show gross structures well, fine structures are obscured by the overlapping of features in depth. Rarely even in thinner sections can particles less than 1 μ in diameter be related to the microstructural pattern, for where the section is thin enough to allow such particles to be clearly resolved, it is too thin to show the structure in which these particles participate. Although sections of uniform thickness are generally considered desirable, sections which taper to a feather-edge in at least one direction are more suitable for the study of microstructures.

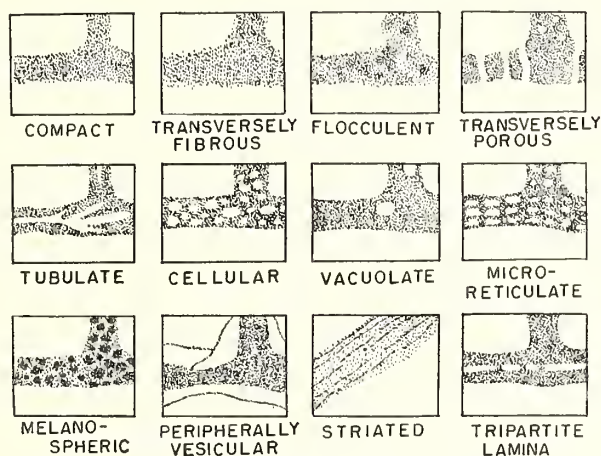
A magnification of 50–100 times has been adopted in this study as suitable for showing microstructures clearly. None of the photomicrographs illustrating this paper is retouched.

Crystallinity and Preservation. Most Palaeozoic stromatoporoids have been preserved by the infiltration of the highly porous galleries by calcite-depositing water. Coenostea are infiltrated in whole or part by calcareous mud but these are very rare. Specimens in which the galleries are now empty have commonly been silicified or dolomitized and have in the process lost all but their grossest structure. In those stromatoporoids that are preserved in the greatest detail the crystal boundaries of the calcite mosaic show no relationship to the tissue of the fossil. Crystals are usually large and their boundaries cross pillars and laminae indiscriminately. The orientation of the crystals in this mosaic is random and therefore growth did not take place in optical continuity with the calcite laid down by the organism. The whole coenostea of these specimens must have been faithfully replaced and filled as a unit by infiltrating lime-rich waters, probably soon after burial when the passage of water through the sediment was at a maximum. St. Jean (1962) drew attention to this form of preservation in *Stictostroma* from Ontario.

In other specimens crystallization of the calcite filling the galleries has been controlled by the structure of the fossil. First a coating of small crystals was laid down on the edges of the galleries. Later the central areas of the galleries were filled in with coarser, clearer crystals of calcite. In still other states of preservation the galleries seem to have been filled with a single generation of coarse crystals and the tissue replaced by a finer

crystal mosaic. The galleries of many Mesozoic sphaeractinoids are filled with a single generation of calcite crystals and the edge of their fibrous tissue is the sharp boundary of these crystals. Some of the specimens, however, seem to have a thin, clear line of crystals between the fibres and the coarse crystals of the galleries. This thin zone is optically related to the fibres of the tissue.

The calcite in stromatoporoids from structurally disturbed rocks is commonly a coarse mosaic of crystals with twin lamellae on which the outline of the tissue is superposed. The microstructure in such specimens is almost always obliterated and the tissue may be so diffused that even the gross structure is lost. Yet some such recrystallized specimens retain the structure clearly outlined in even, very finely dusty, tissue. The stromatoporoids from Devon show a great variation in this respect; some are completely obscured, others retain the structure and rarely traces of the microstructure.



TEXT-FIG. 1. Stromatopore microstructures.

Summary of Microstructures. Descriptions of the microstructures of stromatoporoids have generally been interpretive and not objective. Detailed description of the highly magnified tissue is uncommon in papers on this group. The small size and indifferent preservation of these microstructures seem to have discouraged objectivity and encouraged idealization so that they have been described in terms of what they might have been rather than what they are now.

The several types of microstructure that have been recognized are listed below and are briefly described. They are considered in more detail in following sections or under the appropriate genera. The smallest elements of microstructure are dark particles of irregular shape and unknown composition from 1 to 5 μ in diameter. These particles are called 'specks' (after Nicholson 1886) and considered in more detail below. Through the co-operation of Drs. Erik Flügel, Heldur Nestor, and D. Le Maître the equivalent terms in German, Russian and French are included in this summation. These equivalent terms were requested by circulating to these palaeontologists a sheet illustrating the various microstructures in photographs and drawings, and briefly describing them in English. French equivalents were also extracted by the writer from Lecompte's (1951-2) monograph. Most of these microstructures are illustrated diagrammatically in text-fig. 1.

1. *Compact* (German—kompakt; Russian—плотная; French—compacte). Tissue composed of evenly distributed specks or evenly coloured calcite.
2. *Transversely fibrous* (German—quer-fibrös; Russian—поперечноволоконистая; French—fibreuse). Tissue traversed by vague lines caused by the alignment of specks or by crystal boundaries.
3. *Water jet* (German—wasserstrahlartig or radialstruktur; Russian—перистоволокнистая; French—en jet d'eau). Tissue marked by fibres that spray outwards and upwards from a central zone.
4. *Flocculent* (German—flockig; Russian—хлопьевидная; French—spongieuse). Tissue composed of unevenly distributed specks or colouring.
5. *Transversely porous* (German—quer-porös; Russian—поперечнопористая; French—poreuse). Tissue traversed by pores which open into the galleries.
6. *Tubulate* (German—mit Röhren; Russian—трубчатая; French—tubuleuse [Le Maitre], tubulée [Lecompte]). Tissue contains curved and branching tubes, commonly horizontal.
7. *Cellular* (German—zellig; Russian—ячеистая or целлюлярная; French—celluleuse [Le Maitre] cellulaire, alvéolaire [Lecompte]). Tissue filled with closely spaced subspherical voids. This term has also been translated in German as 'makulat', equivalent to Galloway's (1957) 'maculate'.
8. *Vacuolate* (German—mit Vacuolen; Russian—кавернозная; French—vacuolaire). Tissue contains subspherical voids, larger and more distinctly spaced than cellules.
9. *Microreticulate* (German—mikroretikulat; Russian—тонкорешетчатая; French—microréticulée). Tissue contains cellules arranged in vertical and horizontal series.
10. *Melanospheric* (German—melanosphärisch; Russian—пятнистая or крапчатая). Tissue filled with dark subspherical groups of specks.
11. *Peripherally vesicular* (German—randlich vesikular; Russian—краевопузыристая; French—à zone externe vesiculaire [Le Maitre], caniculo-cellulaire marginale [Lecompte]). Structural elements bordered by a layer of vesicles or a continuous membrane.
12. *Striated* (German—gestreift; Russian—полосатая; French—striée). Tissue filled with dark or light, thin, rod-like bodies.
13. *Tripartite laminae* (German—dreigeteilte Lamina; Russian—трехслойная ламина; French—trilaminaire [Le Maitre], Lamelle bipartite [Lecompte]). Lamina has a central light zone that may break up into a line of cellules.
I propose to call the microstructure of laminae which are occupied by a single plane of cellules 'ordinicellular' (Latin: row of small chambers).
14. *Meshed fibre* (French—? fibrillaire [Lecompte]). Lamina longitudinally fibrous, composed of intermeshed fibres and dissepiments. (Used only by Lecompte (1956) for *Synthetostroma*).

In a recent letter Yavorsky indicated that he uses translations of Nicholson's terms to describe the microstructure of the stromatoporoids. He believes that the word 'compact' adequately describes the microstructure of all the genera in Nicholson's hydroactinoid group. For the microstructure of *Stromatoporella* he uses 'thread-like' or 'stream-like'. Yavorsky (1962) recently illustrated his concept of the microstructure of many stromatoporoid genera.

Specks and Speckled Tissue. When appropriately thin sections of many stromatoporoids are magnified about 100 times the tissue can be seen to be crowded with dark irregular particles which Nicholson (1886) referred to as specks. Nicholson believed these to be fillings of minute pores or tubules and Lecompte (1951, p. 16) also favoured this interpretation. Galloway (1957, p. 361) noted that their composition is unknown, that they are probably deposited by infiltrating water and may consist of iron oxide, sulphide, or organic carbon. St. Jean (1962) described the specks in *Stictostroma* in detail but referred to them as flecks. He noted their movement and their tendency to clump into what he called pseudomaculae. Lecompte (1951) believed them to be centres of carbonaceous pigment.

The specks are highly irregular in shape but rarely do they seem to be tubular (Pl. 14, fig. 1). As they are only $0.5\text{--}5\ \mu$ in diameter determination of their composition is difficult. The electron probe may offer a hope for a solution of this problem. St. Jean (1962) reported the probable presence of an amino acid in a Palaeozoic stromatoporoid. Such a compound was probably located in the dark specks of the tissue but its position remains conjectural as the analysis was made by dissolving the whole coenosteum.

The specks seem to be bodies of carbonaceous matter that have been concentrated from the diffuse organic matter originally present throughout the calcite crystals secreted by the organism. The aragonite hard parts of recent hydrozoans do not contain much organic matter. However, Moseley (1891) quoted analyses of skeletal tissue of *Millepora* showing several per cent. of organic matter and perhaps the stromatoporoids incorporated more within their tissue than their modern representatives. Many modern hydrozoans have plant parasites in their hard parts but the specks of stromatoporoid tissue are too evenly and universally present to be the remains of such parasites.

Some well-preserved specimens show no specks but the tissue is distinguished from the clear gallery fillings by its darker, usually brownish, colour or by a milkiness that cannot be resolved into particles. Such tissue is common in Devonian stromatoporoids from Germany and Canada. This darker tissue may have specks superposed upon it or more commonly the concentration of specks alone distinguishes the tissue from the galleries. The coloured, speckless tissue is believed to be close to the form in which it was secreted before the specks emerged.

In different stratigraphic units the stromatoporoids are preserved differently. The stromatoporoids from Devon are recrystallized; those from the Silurian of Shropshire have widely spaced dark specks and crystal mosaics independent of the structure; those from the Devonian of the central United States are coarsely speckled and few show clear cellular structures; those from the Devonian of western Canada either have very fine specks closely set or brown coloured speckless tissue. In well-preserved stromatoporoids the edge of the speckled tissue is sharply defined. The specks, however, are capable of movement during such processes of preservation as the lining of cavities, infiltration of voids, replacement, and recrystallization. Whether the specks themselves move or whether the diffuse organic matter from which they eventually emerge does so is difficult to determine now, but the latter seems more likely. The end result is that the specks seem to have moved (Pl. 15, fig. 2). As St. Jean (1962) has shown they move out into the galleries, making the boundary of the tissue gradational and diffuse. They also show concretionary tendencies and clump into what St. Jean (1962) has called pseudomaculae, but which are here called melanospheres and are discussed below.

Transverse Fibrosity and Water Jet Microstructure. Fibrous microstructure is widespread in a wide variety of genera of stromatoporoids. This fibrosity locally seems to be caused by the alignment of the specks across the elements of structure and locally by the development of transverse intercrystalline boundaries. Although transverse fibrosity is more marked in some genera such as *Anostylostroma* (Pl. 14, fig. 4), *Amphipora*, and *Stictostroma*, it may develop under appropriate conditions in almost any tissue. In tangential section such fibrosity may seem to be radial in the pillars, or patches of tissue may show a direction of fibrosity unrelated to neighbouring patches. In some states of preservation the alignment of specks into a fibrous microstructure develops

over relatively large areas of tangential sections either regionally aligned in a certain direction or in swirls. Tangential sections of *Syringostrova* from the central United States commonly show this type of fibrosity.

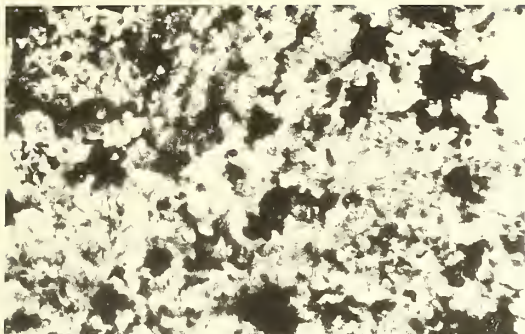
The long rod-like pillars of some genera show fibres radiating upwards and outwards from their axes. This produces a water jet or feather structure in longitudinal section and a radial structure in tangential section. Such a fibrosity is particularly characteristic of Mesozoic sphaeractinoids (Steiner 1932, Hudson 1958) but occurs in certain states of preservation in many Palaeozoic genera and seems in the latter to be a microstructure formed during preservation. It occurs in two positions: (a) within the tissue, and (b) within the gallery space. If it occurs in the tissue of the pillars it may be accompanied by an axial dark line as in those specimens identified by Nicholson as *Stromatopora beuthii* (not *Hermatostronia beuthii* (Bargatzky) of Lecompte, with which only one or two of Nicholson's specimens agree) or in *Actinostroma clathratum* Nicholson. I have also observed water jet microstructure in some species of *Taleastrova* and *Actinostroma*. One of Nicholson's specimens of *Stromatopora bucheliensis* (Bargatzky) (Nich. 97) shows (Pl. 14, fig. 2) that water jet fibrosity may form in cellular tissue completely unrelated to the position of the cellules. A water jet structure has also been described by Stearn (1961, 1962) in *Taleastrova? confertum* Stearn, *Syringostrova bifurcum* Stearn, and *Trupetostroma pycnostylotum* Stearn, and may be seen in several poorly preserved stromatoporoids in the Nicholson collection with thick, closely set pillars.

In all these species the fibrosity appears to be caused by the outward growth of fibrous crystals from an axis. Galloway (1957, p. 464, pl. 31, fig. 15) illustrated a microstructure like a water jet in *Syringostrova densum* Nicholson caused by the spray-like arrangement of melanospheres in the pillars. This microstructure is not comparable with that shown by specimens described above.

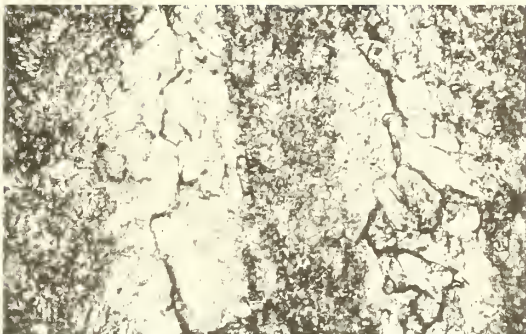
Water jet fibrosity in the galleries is well illustrated by specimens of *Parallelopora dartingtonensis* (Carter) from Devon which Nicholson (1886) described as 'reversed'. In these the tissue is light coloured or clear and the calcite of the galleries and astro-

EXPLANATION OF PLATE 14

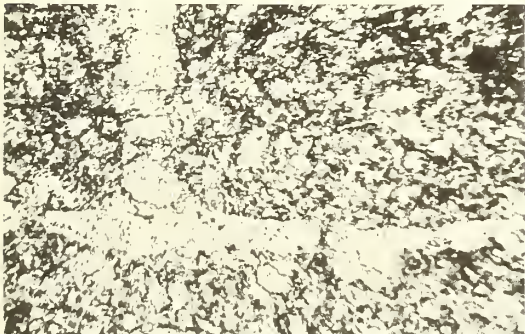
- Fig. 1. *Syringostrova subfuscum* Galloway and St. Jean (UNC 294-88). Vertical section of paratype, $\times 250$, showing the specks made of irregularly distributed dark matter. Middle Devonian, 5 miles E. of Logansport, Indiana.
- Fig. 2. *Stromatopora bucheliensis* (Bargatzky) (Nich. 97). Vertical section of holotype, $\times 100$, showing cellular microstructure and suggestion of water jet fibrosity in the pillars. Middle Devonian, Büchel, Germany.
- Fig. 3. *Anostylostroma arvense* Parks (UNC 272-16). Vertical section, $\times 100$, showing lack of fibrosity in tissue surrounded by sediment. Middle Devonian, Marblehead, Ohio.
- Fig. 4. *Anostylostroma laxum* (Nicholson) (UNC 282-52). Vertical section, $\times 100$, showing transversely fibrous laminae and darker pillars. Middle Devonian, 5 miles NW. of Columbus, Ohio.
- Fig. 5. *Stromatopora mononensis* Galloway and St. Jean (UNC 278-21). Vertical section of holotype, $\times 100$, showing clear microlaminae traversing speckled tissue. Middle Devonian, 2 miles W. of Monon, Indiana.
- Fig. 6. *Clathrodictyon vesiculosum* Nicholson (Nich. 218a). Vertical section, $\times 100$, showing compact, speckled tissue. Middle Silurian, Much Wenlock, Shropshire.
- Fig. 7. *Stromatopora typica* Rosen (Nich. 57a). Tangential section, $\times 100$, showing transitional stage from cellular to melanospheric tissue. Middle Silurian, Kaugatoma, Oesel Island.
- Fig. 8. *Stictostroma danmoniensis* (Nicholson) (Nich. 355). Vertical section, $\times 100$, showing flocculent tissue with slight development of fibrosity. Middle Devonian, Teignmouth, Devon.



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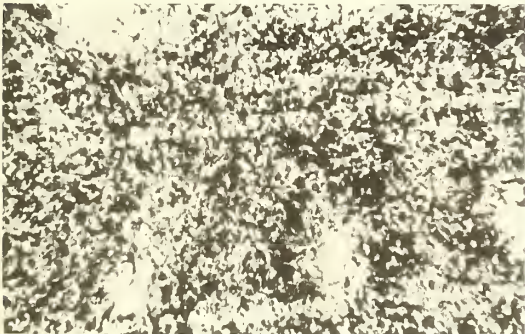
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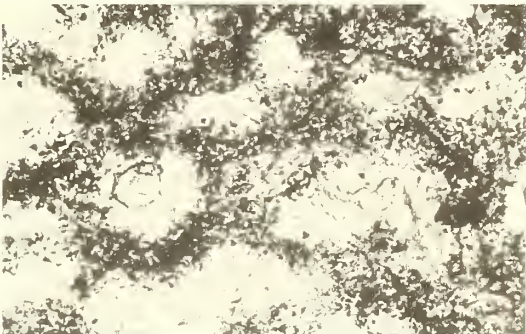
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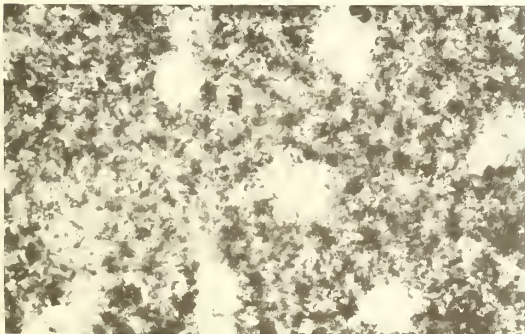
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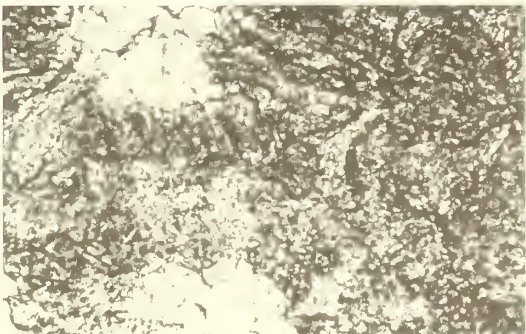
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rhizal canals, which is normally clear, is darkly stained apparently by bituminous matter. Nicholson's suggestion that the filling is a recrystallized calcareous mud does not seem likely. This dark filling shows a fibrous crystallinity in which the crystal boundaries curve outwards from the axis of the galleries or canals and the margins of the tissue are irregular. This kind of preservation is uncommon but its existence confuses the interpretation of specimens common in the Devonian of Alberta (Stearn 1963, p. 667) whose whole structure consists of contiguous water jets.

The examples given above establish that fibrosity due to crystalline boundaries occurs in a variety of otherwise unrelated genera and may develop during the preservation of the specimen. In some genera such as *Anostylostroma*, *Stictostroma*, and *Amphipora*, transverse fibrosity is almost universally present and in such genera may be of systematic importance. In some specimens of *Anostylostroma* in which the galleries have been locally filled with calcareous mud rather than crystalline calcite (Pl. 14, fig. 3), the transverse porosity common in the genus has not developed and the tissue is cryptocrystalline and without specks. This suggests that transverse porosity even in these genera may be a feature of preservation and should be used with care in taxonomy. Further research may show that transverse porosity due to crystalline boundaries is a phenomenon of preservation and transverse porosity due to alignment of specks is a primary microstructure.

In Mesozoic sphaeractinoids the fibres curve outwards from an axial strand (that may or may not be darker) to meet the border of the tissue perpendicularly (clinogonal of Hudson 1958) or extend straight out from the axial strand (orthogonal of Hudson 1958). This fibrosity is invisible in plane light in certain states of preservation but under crossed nicols it is revealed as due to the alignment of fibrous crystals. In places dark specks may also be aligned with the fibrosity but it is fundamentally crystalline.

Flocculent Microstructure. In many stromatoporoids the speckled tissue is neither fibrous nor homogeneous but the density of the specks and colour is not uniform. Such tissue looks blotchy and has the texture of curdled cream (Pl. 14, fig. 8). Galloway and St. Jean (1957) referred to it as flocculent tissue. It is common in thick stromatoporoid tissue such as occurs in *Stromatoporella* and is further discussed under that genus.

Cellular, Melanospheric, Maculate, and Microreticulate Microstructure. The tissue of *Stromatopora* and related genera contains spherical clear areas or dark areas (Pl. 18, figs. 2, 4). Galloway (1957, p. 355) listed ten terms which writers have used to describe the microstructure of these genera and all of them imply that the tissue encloses vacuities. Nicholson (1886, p. 36) referred to the microstructure as 'dotted or porous' but leaves no doubt elsewhere in his monograph that he understood that the tissue contained sub-spherical voids. Galloway (1957), and Galloway and St. Jean (1957) substituted for Nicholson's word 'dotted' the term 'maculate', and described the tissue as not porous or cellular but dotted either with light maculae on a dark field or vice versa. Galloway wrote (1957, p. 363) 'The maculae are not pores but dots: e.g. light or dark', yet (p. 358) he referred to the tissue of *Stromatopora* as 'spongy', which seems to imply pores. Galloway conceived the maculae as spheres in which dark matter is concentrated at the periphery so that in thin section they typically have a light centre. He believed that the expansion of the clear centres gave rise to clear maculae, that is, dark tissue with lighter dots. None of the specimens of *Stromatopora* examined by me show distinct annular

structures. In uncommon states of recrystallization specks have moved towards the peripheries of crystals making them light in the centre and dark at the edge but this is not the microstructure referred to by Galloway. Galloway (1957, p. 363) described the maculae as being 0.2–0.3 mm. in diameter but this must be a misprint for 0.02–0.03 mm. for below he stated that larger ones may be 0.03–0.06 mm. He described, however, structures as large as 0.13 mm. as maculae (1960, p. 634).

The maculate concept of microstructure seems to be based on examination of the stromatoporoids from the central United States which commonly show the maculae as dark dots against a light background. Well-preserved specimens from Europe of *Stromatopora* and related genera show spherical vacuities or cellules in darker tissue. However, spherical clusters of dark specks in lighter tissue do occur in the tissue of many European specimens. Galloway has used the term maculate to apply to tissue containing light and dark spheres but these are two different microstructures and each needs a descriptive term. The dark spheres in lighter tissue are called melanospheres (Stearn 1965) and the microstructure they define is melanospheric. The tissue with spherical vacuities (the light maculae of Galloway and St. Jean) is called 'cellular' as suggested by Lecompte (1952, 1956) and others.

That melanospheric and cellular microstructures can be different states of preservation of the same original tissue is indicated by the following:

1. Different specimens of the same gross structure may be cellular or melanospheric.
2. Within the same coenosteum or thin section melanospheric and cellular tissue may coexist.
3. In some states of preservation a single field under the microscope may be interpreted as either melanospheric or cellular. Such fields present an optical illusion. If the observer concentrates on the light areas, they seem to be holes in the dark background; if he concentrates on the dark areas, they seem to be dots on a light field.

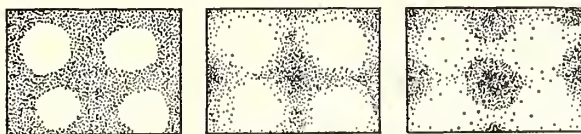
How then are the two microstructures related? Examination of the transition from one to the other in the same specimen shows that the filling of the cellules by organic matter does not produce melanospheric tissue. The tissue of the best preserved specimens which approaches the microstructure of the tissue secreted by the organism contains closely set subspherical vacuities (cellules). In such tissue the largest masses of dark matter would be between four closely packed cellules and would be connected around the cellules by tenuous films of dark matter to adjacent large masses. In the process of preservation the films of dark matter connecting the larger masses are either diffused as the cellules enlarge or else their dark matter migrates to the larger intercellular masses leaving a light tissue with subspherical dark masses of specks, the melanospheres. Specimens in intermediate stages of this process can be found showing melanospheres with small extensions towards neighbouring melanospheres (Pl. 14, fig. 7). The resulting melanospheres do not occupy the positions of the cellules but intercellular positions (text-fig. 2). The dark matter may be either structureless or resolved into specks.

The proportions of light and dark tissue in cellular and melanospheric microstructures in a given section will depend on several factors, such as:

1. The position of the plane of the section with respect to the microstructure. Different sections of the same random microstructure will give different proportions.

2. The original size of the cellules.
3. The amount of their secondary enlargement.
4. The relationship of the thickness of the section to the size of the cellules or melanospheres.
5. The arrangement of the cellules, whether random or regular.

The appearance of tissue that originally had a cellular microstructure may for these reasons differ widely within sections, between specimens, and between different species.



TEXT-FIG. 2. Transition from cellular to melanospheric tissue.

Unfortunately, melanospheres develop in tissue that was not cellular and are not an infallible sign of originally cellular tissue (Pl. 16, fig. 8). Melanospheric tissue is not rare in such genera as *Stromatoporella* and *Stictostroma* and has been interpreted as cellular tissue by some investigators. Even such compact genera as *Anostylostroma* may show isolated areas of melanospheric tissue. These subspherical masses of specks in 'non-maculate' genera have been called pseudomaculae by St. Jean (1962) but are regarded as melanospheres in this paper (Pl. 15, fig. 3). The only fallible index to cellular tissue is the appearance of closely spaced spherical voids in well-preserved specimens but stromatoporoids whose tissue is evenly and extensively melanospheric are likely to have had cellular tissue.

Melanospheric tissue seems to develop in compact genera through the concretionary tendencies of the specks. Flocculent tissue may be an intermediate stage in the transition from compact to melanospheric tissue. The tendency for the dark matter to gather into balls, which is evident in the progressive changes taking place in both cellular and compact tissue, has no obvious explanation.

In one type of cellular tissue the cellules are arranged in vertical and horizontal series and the dark or speckled tissue between the cellules forms a crude three-dimensional lattice. This microstructure is called microreticulate (Pl. 18, fig. 3). Nicholson (1886) used the term 'continuously reticulate' to refer to tissue in which pillars and laminae blend to form a network but the term microreticulate refers to a feature of much smaller scale. Microreticulate tissue gives rise to melanospheric tissue and may also give rise to tissue containing rod-like bodies of dark matter as in *Parallelopora*. The various manifestations of this tissue and its relationship to microlaminae are discussed below under *Stromatopora*, *Syringostroma*, and *Parallelopora*.

Other Microstructures. Other microstructures which are not as widespread as those discussed above are considered further under appropriate genera below, as follows:

- Transversely porous—*Stromatoporella* and *Stictostroma* (Pl. 16, fig. 5)
- Tubulate—*Stromatoporella* (Pl. 16, fig. 3)
- Vacuolate—*Trupetostroma* (Pl. 17, fig. 1)

Tripartite lamina and ordinicellular tissue—*Stromatoporella*, *Stictostroma*, *Trupestostroma* (Pl. 16, fig. 4)

Striated—*Stachyodes* (Pl. 18, fig. 8)

Peripherally vesicular—*Hermatostroma* (Pl. 17, fig. 4).

TISSUE REVERSAL

In some specimens the galleries have been filled with dark sediment and the tissue therefore is lighter than the galleries instead of the galleries being clear and the tissue dark. Such tissue reversal is not difficult to understand. A more puzzling phenomenon is the occurrence of certain microstructures in either a 'white-on-black' or a 'black-on-white' form. Genera that are characterized by tripartite laminae include *Stictostroma*, *Trupestostroma*, *Stromatoporella*, and *Clathrocoilona*. The central layer of the laminae is normally light and the outer layers darker. Well-preserved specimens of *Stictostroma* and *Stromatoporella* suggest that the central light zone is the result of the joining during preservation of a line of cellules along the axis of the lamina. In all these genera the central zone may also appear to be darker than the lateral ones. In some specimens of *Stromatoporella kirki* (Galloway and St. Jean) different laminae in the same section may show a dark or light axial line. In *Clathrocoilona restricta* (Galloway and St. Jean) laminae with a light central zone may have this replaced laterally by a dark line which looks like bituminous matter filling a crack. In these specimens the dark axial line may be explained as an organic filling of a porous zone but when one group of specimens consistently has dark axial zones and another group light axial zones, doubts arise as to whether these were the same structures originally.

In several species of *Stromatopora* and *Syringostroma* fine microlaminae are represented by dark lines in the tissue (Pl. 17, fig. 7). In the species *Stromatopora mononensis* (Galloway and St. Jean) (Pl. 14, fig. 5) and *Syringostroma bicrenulata* (Galloway and St. Jean) the microlaminae are clear zones traversing a generally dense, speckled and melanospheric tissue. Are the clear zones the same microstructure as the dark microlaminae in a different state of preservation? How were they formed when the tissue was secreted? In one specimen of *Labechia conferta* from the Nicholson collection (Nich. 266a) most of the cysts are black lines which have a zone into which the specks have migrated on either side. In one group, however, the zones enclose clear tissue as if after the specks had spread into the galleries the cyst itself had been replaced by clear calcite. In some specimens that have regular laminae crossing pillars, the laminae between the pillars are a dark speckled layer but where they cross the pillars they are represented by a clear zone in the tissue. More work is needed on these phenomena before an explanation can be offered.

Related to these unsolved problems of tissue reversal are problems of secondary and primary tissue and the superposition or continuity of pillars. Galloway (1957) distinguished primary tissue which forms the darker, finer, core structures of laminae and pillars from secondary tissue which is lighter in colour, less dense in texture, commonly porous and coats the primary tissue, tending to fill in the galleries. For example, he pictures the structure of *Stromatopora* as made up of primary microlaminae coated with secondary maculate tissue which fills most of the galleries. Although the distinction between two types of tissue may be valuable, the assumption that one type of tissue was

laid down first and the other followed perhaps at a later stage is unjustified. In addition, the adjective 'secondary' carries the suggestion of tissues deposited by inorganic agencies after the organism was dead. Where a microlamina is covered with lighter tissue it is referred to as clothing or coating tissue in this paper.

In genera with distinct long pillars and laminae, systematic importance has been placed on whether the pillars are interrupted by the passage of the laminae and composed of superposed segments (e.g. *Trupetostroma*, *Gerronostroma*) or whether they are continuous through the laminae (e.g. *Actinostroma*). Doubt is thrown on the validity of this distinction by many thin sections in which pillars seem to be continuous through laminae in parts and broken into segments by laminae in other parts. Although poor preservation may obscure the interruption of the pillars by the laminae, variations in preservation alone cannot explain the differences in the expression of this feature. In certain parts of coenostea growth of pillars seems to have been interrupted by the deposition of a lamina. In other parts the pillars seem to have grown continuously, perhaps secreted by cells elevated above the general level of the sheet of living matter, while periodically a lamina was deposited below and around them.

DISCUSSION OF GENERA

In the following section the microstructures of the major genera of stromatoporoids are described and the definitions of the genera reviewed. Holotypes of the type species of the following genera were examined in the course of this study: *Actinodictyon*, *Actinostroma*, *Anostylostroma*, *Clathrodactyon*, *Cystostroma*, *Dendrostroma*, *Hammatostruma*, *Hermatostroma*, *Idiostroma*, *Labechia*, *Labechiella*, *Lophiostroma*, *Parallelopora*, *Pseudoactinodictyon*, *Rosenella*, *Stachyodes*, *Stictostroma*, *Stromatoporella*, *Stylodictyon*, *Syringostroma*, *Taleastroma*, *Trupetostroma*. Types of lesser value of the type species of the following genera were examined as indicated: *Amphipora* (topotype), *Aulacera* (topotype), *Clathrocoilon* (hypotype), *Cryptophragmus* (topotype), *Gerronostroma* (paratype), *Stromatopora* (topotype). Holotypes of the type species of the following genera have not been seen by the writer and most of these genera are not included except briefly in the following discussion: *Atelodictyon* Lecompte, *Cambrostroma* Vlasov, *Clathrostroma* Yavorsky, *Clavidictyon* Sugiyama, *Ferestromatopora* Yavorsky, *Intexodictyon* Yavorsky, *Korovinella* Khalfina, *Paramphipora* Yavorsky, *Praeactinostroma* Khalfina, *Synthetostroma* Lecompte, *Vicunostachyodes* Yavorsky, some recently described Russian genera, and several Labechioids. No attempt is made to review synonymies of genera or the history of their usage as both have been done by Galloway (1957) and Lecompte (1951-2). Structures such as dissepiments, astrorhizal canals, and surface features which are not generic characters have been eliminated from the diagnoses and discussions. Only a few of the critical species of each genus are mentioned.

The highly idealized three-dimensional drawings of the structure and microstructure of many of the genera (text-figs. 3, 4, 6-10, 12-15) represent my interpretation of the patterns shown by the unretouched photographs at a magnification of $\times 50$. In genera with well-defined laminae only a single lamina and interlaminar space is illustrated by the stripping of adjacent laminae and their associated pillars. Where the continuity of pillars is important in the structure, these are illustrated on both sides of the lamina. The front and side surfaces are vertical sections. The top surface is a tangential section

which intersects the pillars near their tops at the front and converges on the lamina toward the back, cutting it tangentially at the back of the diagram.

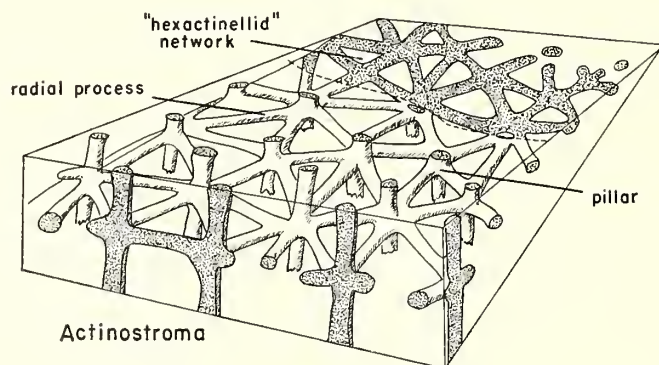
Problems of classification are outside the scope of this paper. The genera have been arranged in an order which places related genera as close together as possible.

ACTINOSTROMA Nicholson

Text-fig. 3

Type species: A. clathratum Nicholson

Coenosteum composed of long continuous pillars which at intervals give off horizontal rod-like radial processes. Processes join neighbouring pillars forming net-like laminae. Tissue compact, in a single layer in the pillars, processes, and laminae.



TEXT-FIG. 3. $\times 50$.

This genus is narrowly defined and was fully revised by Flügel (1959). In general the tissue is evenly speckled throughout both pillars and laminae but the specks of Silurian species seem to be larger (approx. $1-5\ \mu$) than the Devonian ones (less than $1\ \mu$). The specks in the tissue move out into the galleries and tend to become aligned perpendicular to the edge of the tissue to produce a fibrous microstructure. When the fibrosity is well developed the pillars may show fibres bending upwards and outwards from the axes (water jet microstructure). Such a microstructure is shown by the type specimen of *A. clathratum* Nicholson in which the fibrosity is outlined not only by the position of specks but also by fibrous crystals following the same pattern (Pl. 15, fig. 1). The pillars in this specimen, and not uncommonly in others of the genus, are lighter in colour than the laminae. Pillars with water jet microstructure are radially fibrous in tangential section.

In parts of the type vertical sections the laminae appear to be continuous; in other parts they appear as a series of dark granules depending on the direction in which the network laminae are cut. Specimens of *A. bifarium* Nicholson and *A. verrucosum* (Goldfuss) also show water jet microstructure. The pillars of *A. bifarium*, *A. clathratum*, *A. expansum* (Hall and Whitfield), and *A. verrucosum* show an axial dark zone where specks are concentrated, or more rarely a light zone. Whether the axial zone is light or dark does not seem to be significant, for some specimens of *A. clathratum* from the Northwest Territories of Canada show both patterns. Undoubtedly this axial concentration

of dark matter is related to the water jet microstructure, a relationship that is evident also in the Mesozoic sphaeractinoids. The tissue of *Actinostroma* may also be flocculent. Ripper (1938) suggested that species of one group of *Actinostroma* (that of *A. stellulatum*) may have porous pillars. One of her new varieties, *A. stellulatum distans*, does show pores in the tissue of the pillars. However, these specimens do not belong to the genus *Actinostroma* but are here placed in the genus *Gerronostroma* discussed below.

Radial arms are given off by the pillars to form a network which in tangential section has been referred to as the 'hexactinellid network'. This network is the *sine qua non* of *Actinostroma* (and *Atelodictyon*) but unfortunately in many specimens it is destroyed or modified during the process of fossilization. When the network is poorly preserved the genus *Actinostroma* is easily confused with *Gerronostroma*, but the latter has continuous laminae pierced by transverse pores and pillars that are commonly interrupted by the laminae. Several species described as *Actinostroma* should be assigned to this genus and several specimens in the Nicholson collection belong in it (see below under *Gerronostroma*). *Actinostroma* resembles *Atelodictyon* closely and differs only in the continuity of its pillars through more than one interlaminar space. *Actinostroma stellulatum* (Nicholson) is not typical of the genus. The lectotype (Nich. 170) shows pillars with radial arms in tangential section; however, they do not unite regularly to form a continuous network, but rather become very numerous in the laminae, forming a fibrous mat. The laminae in vertical section are persistent and appear to be solid. The pillars are generally confined to a single interlaminar space, but locally they seem to be either superposed or pass through several laminae. The type specimen has a compact tissue which is somewhat flocculent and shows a tendency to break down into melanospheres in the pillars. The species is closely related to *Atelodictyon* but its superposed pillars make its retention in *Actinostroma* possible.

Flügel (1958) placed *Actinostroma astroites* (Rosen) in a separate subgenus of *Actinostroma* called *Densastroma*. The structure of this species is so unlike that of other species of *Actinostroma* and superficially like that of *Stromatopora* that its separation from the rest of the species of *Actinostroma* is desirable. The laminae and pillars of topotypes in the Nicholson collection are very thin and the tissue is finely speckled like that of many Silurian stromatoporoids. The grid of pillars and laminae is so fine that the slightest diffusion obliterates the structure entirely.

Nestor (1964) separated the group of *Actinostroma intertextum* Nicholson from the rest of the genus on the basis of the lack of regularity in the giving off of the radial processes. The microstructure of the new genus, *Plectostroma* Nestor, determined on the basis of the type of *A. intertextum* (Nich. 188) is compact, with speckling of the tissue well developed.

ATELODICTYON Lecompte

Type species: A. fallax Lecompte

Coenosteum composed of well-defined pillars and laminae. Pillars confined to a single interlaminar space, commonly incomplete and branching, giving off at the top horizontal processes which join as a network, or in chain-like groups to form the laminae. Laminae fundamentally net-like, typically discontinuous in vertical section. Horizontal processes may be thickened so that laminae appear to be a sheet of tissue with round closely spaced foramina. Tissue compact.

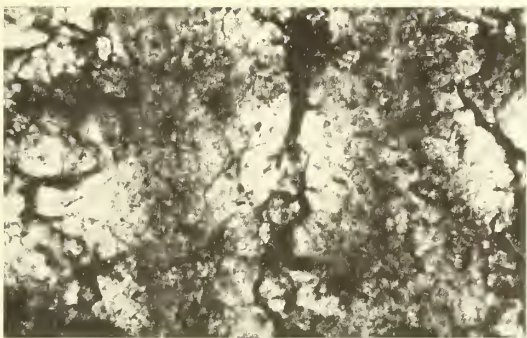
In proposing this genus Lecompte (1951) included in it a group of Silurian and Devonian species formerly described as *Clathrodictyon* and described three new Devonian species. Both he and Galloway (1957) emphasized its relationship to *Clathrodictyon*, yet in the way the laminae are formed it is fundamentally different from the whole of the Clathrodictyonidae and similar to the Actinostromatidae. I was unable to see the type specimens of *A. fallax* but they are figured and described by Lecompte (1951) and by Galloway and St. Jean (1957). In the type species the pillars are simple short columns and commonly superposed but in other species, particularly those from North America (*A. intercalare* Galloway and St. Jean, *A. stelliferum* Stearn, *A. ordinatum* Stearn), the pillars tend to divide and branch, to be oblique and incomplete.

The laminae of *A. fallax* are apparently a single layer of tissue with bordering darker zones in places. The laminae in vertical section appear to be solid, but such a structure could result from the cutting of the net-like laminae shown in tangential section only if the vertical sections pictured are thick. In *A. intercalare*, *A. stelliferum*, and *A. ordinatum* the laminae break up in vertical section into a series of granules—the cut ends of the radial processes which form the laminar network. In *A. intercalare* the aligned granules form a single layer but in *A. stelliferum* they are coated on either side with lighter coloured continuous tissue. The pillars of *Atelodictyon* are compact and, in vertical section at least, not porous. However, in tangential sections of several species, including the type species, an open space appears in the centre of each pillar where it splits into horizontal processes. Apparently the pillar has a slight closed depression where the processes diverge.

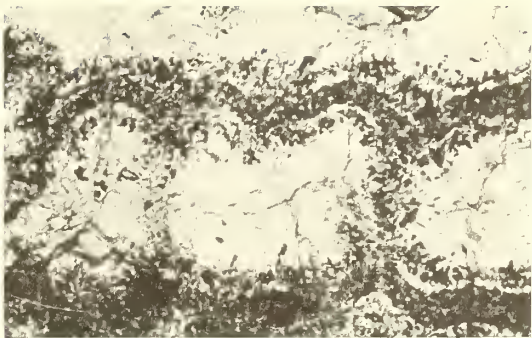
Galloway (1957) restricted this genus to the Middle Devonian but Lecompte (1951) included several Silurian specimens in it. The species of *Atelodictyon* described as possibly Silurian by Ripper (1933), such as *Clathrodictyon chapmani* (Ripper) and *Clathrodictyon regulare distans* (Ripper) (probably = *Atelodictyon distans*), are of Devonian age (Ripper 1938). Several species of *Clathrodictyon* described by Boehnke (1915) from the Silurian drift of northern Germany (such as *C. alternans* Boehnke, *C. spatiosum*

EXPLANATION OF PLATE 15

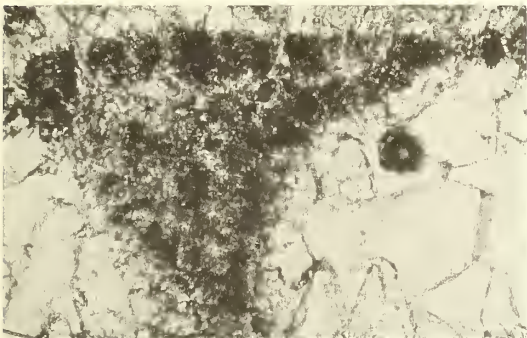
- Fig. 1. *Actinostroma clathratum* Nicholson (Nich. 141). Vertical section of lectotype, $\times 100$, showing compact pillars and laminae; water jet fibrosity is present but does not show well on the photograph. Middle Devonian, Gerolstein, Germany.
- Fig. 2. *Clathrodictyon striatellum* (d'Orbigny) (Nich. 246). Vertical section, $\times 100$, showing clear zone separating the specks of the laminae from those migrating out into the galleries. Middle Silurian, Dorington, Shropshire.
- Fig. 3. *Anostylostroma hamiltonensis* Parks (ROM 16536). Vertical section of holotype, $\times 100$, showing flocculent (approaching melanospheric) pillar and transversely porous lamina. Middle Devonian, Alpena, Michigan.
- Fig. 4. *Pseudoactinodictyon vagans* (Parks) (ROM 9376). Vertical section of lectotype, $\times 50$, showing compact pillars and cysts. Middle Devonian, Kelly's Island, Ohio.
- Fig. 5. *Hammatostroma albertense* Stearn (McGill Univ. 38-12). Vertical section of holotype, $\times 50$, showing transversely fibrous laminae and pillar tissue. Upper Devonian, Isaac Creek, Alberta.
- Fig. 6. *Stromatoporella granulata* Nicholson (Nich. 329c). Vertical section of holotype, $\times 100$, showing ordincellular laminae. Middle Devonian, Arkona, Ontario.
- Fig. 7. *Stromatoporella granulata* Nicholson (Nich. 329a). Tangential section of holotype, $\times 100$, showing pattern of cellules in a ring pillar and lamina. Middle Devonian, Arkona, Ontario.
- Fig. 8. *Stromatoporella selwyni* Nicholson (Nich. 330). Vertical section of holotype, $\times 100$, showing microreticulate character of laminae and pillars. Middle Devonian, Port Colbourne, Ontario.



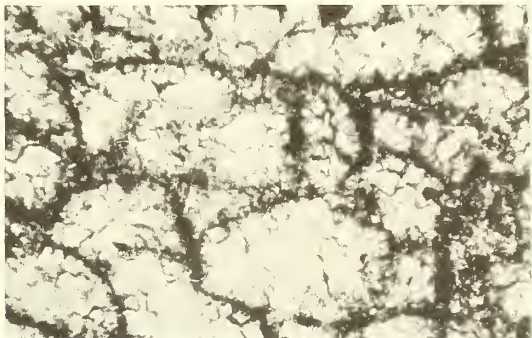
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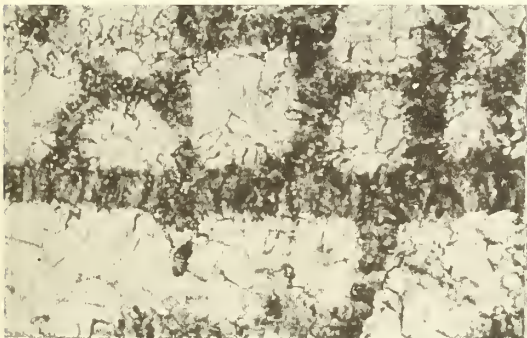
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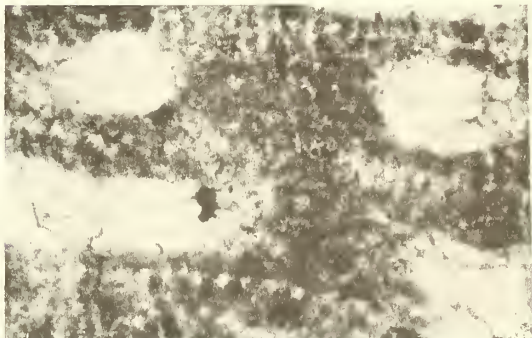
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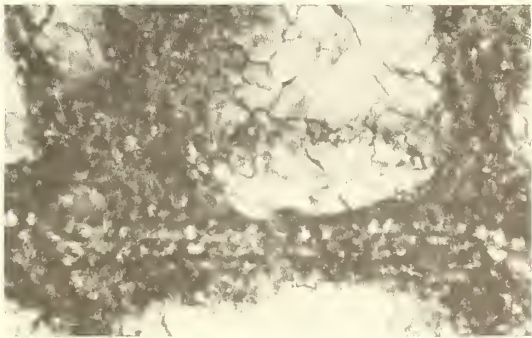
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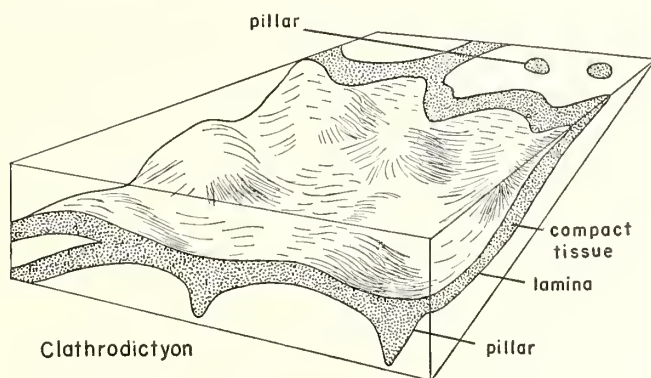
Boehnke, *C. dirsckheimiense* Boehnke) have laminae which are net-like in cross-section and seem to belong in *Atelodictyon*. Their Silurian age is open to doubt. I do not agree with Lecompte's suggestion that *C. linarssoni* Nicholson and *C. carnicum* Charlesworth should be assigned to *Atelodictyon*. As *C. linarssoni* has solid laminae and no suggestion of a network structure there is little justification for assigning it to *Atelodictyon* (Lecompte 1951, p. 127). *C. carnicum* is closer to *Hammatostroma* (see also Flügel 1956, p. 145 footnote). Better preserved specimens of *C. ostiolatum* Nicholson than are in the Nicholson collection from the Silurian of Ontario will probably show that this species is an early representative of *Atelodictyon*. The extension of the range of the genus into the Silurian needs confirmation.

CLATHRODICTYON Nicholson and Murie

Text-fig. 4

Type species: C. vesiculosum Nicholson and Murie

Coenosteum composed of imperforate, continuous laminae, commonly undulant or crumpled, and short pillars that are confined to an interlaminar space. The pillars and laminae are a single uniform layer of compact, commonly speckled, tissue. Where the laminae are bent, the pillars extend from their downward inflexions and are cylindrical in form.



TEXT-FIG. 4. $\times 50$.

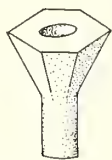
Although the definition of the genus *Clathrodictyon* on the basis of its gross structure is controversial, its microstructure is unequivocal. The type species (*C. vesiculosum*) and all those close to it in structure are composed of tissues with evenly distributed specks in both laminae and pillars. The tissue shows no sign of porosity or cellular microstructure. Fibrosity is not typical but may develop under certain conditions of preservation. In well-preserved specimens the boundaries of the tissue are sharp, but movement of the specks out into the galleries, particularly from the pillars, is common (Pl. 14, fig. 6).

Some specimens show fine dark lines in the laminae. One of Nicholson's specimens (Nich. 449) of *C. linarssoni* Nicholson, and one of *C. regulare* Rosen (Nich. 250) show such a dark concentration of particles in the laminae, but it is apparently produced during preservation as neither is well preserved. Boehnke (1915) described *C. spatiosum* as having central dark lines but from his illustrations this species might better be referred to *Atelodictyon*.

Lecompte (1951) reviewed early work on this genus and recorded the divisions into groups that each investigator had made among the species without recognizing the groups taxonomically. The heterogeneity of the genus may have begun with Nicholson, who first (Nicholson and Murie 1878) defined the genus in terms of undulant laminae giving rise to vesicles, and later (1886) in terms of distinct pillars producing the laminae by giving off radial arms like those of *Actinostroma*.

Lecompte recognized two groups, one with vesicular tissue and one with distinct pillars and laminae but he hesitated to divide these groups into different genera. However, Galloway (1957) restricted *Clathrodictyon* to those species in which the horizontal elements are not laminae but a series of cysts placed end to end and in which the pillars have no separate existence but are the downward continuations of the edges of the cysts. His statement that the tops of the cysts are atypically in straight lines cannot be supported from the type specimens of *C. vesiculosum* from Ohio in which the tops of almost all the convex parts of the laminae are in line and almost uninflected laminae occur locally. Galloway would place those species in which the pillars and laminae are distinct in *Anostylostroma*. However, he restricted this latter genus to the Middle Devonian species with upwardly branching pillars and made no provision for Silurian species such as *C. regulare* Rosen, *C. striatellum* (d'Orbigny) (Pl. 15, fig. 2), and *C. linarssoni* Nicholson, which have well-defined laminae. Nestor (1964) agreed with Galloway's diagnosis of the genus but retained the species listed above within it. As these species are transitional into *C. vesiculosum* they cannot be excluded from the genus and therefore the generic diagnosis of *Clathrodictyon* proposed by Galloway cannot be accepted. Neither is his diagnosis consistent with the dot-like appearance of the pillars in tangential sections of the type and related species. Such dots cannot be derived from cutting a series of cysts. Nevertheless, the genus *Anostylostroma* is a convenient one for Devonian species such as those that Lecompte (1951) referred to his second group of *Clathrodictyon*.

The Silurian species described by Nicholson are all (with the possible exception of *C. ostiolatum*) regarded here as belonging to the genus *Clathrodictyon* as defined above. I cannot agree with Lecompte (1951, p. 167) that *C. crassum* is a *Stromatoporella* as it has neither ring pillars, an axial line of cellules, nor cellular tissue. It is a *Clathrodictyon* with thick, single-layered tissue in which melanospheres have developed locally. The



TEXT-FIG. 5. Diagrammatic sketch of a pillar of *Clathrodictyon striatellum* showing the expanded end and central depression, $\times 50$ approx.

Devonian species described by Nicholson can be assigned to *Anostylostroma* (*C. retiforme*, *C. laxum*), to *Stromatoporella* (*C. cellulosum*), or are indeterminate structures (*C. confertum*).

Tangential sections of some specimens of *Clathrodictyon* in which the laminae bend down to the pillars in a 'V', such as *C. striatellum* and *C. regulare*, show a rectilinear network of light lines in the darker speckled tissue of the laminae. Each polygon so formed represents the head of a pillar and commonly encloses a central clear area. As the pillars of such species spread upwards to meet the lamina they become hollow and encounter adjacent spreading pillars. The interference of these pillars forms a hexagonal network much like that of a honeycomb, for at a level just below the top of the lamina they do not blend but their integrity is maintained by a thin clear line between them. Each pillar is shaped as illustrated in text-fig. 5.

Nestor (1964) established the genus *Ecclimadictyon* for those species of *Clathrodictyon*,

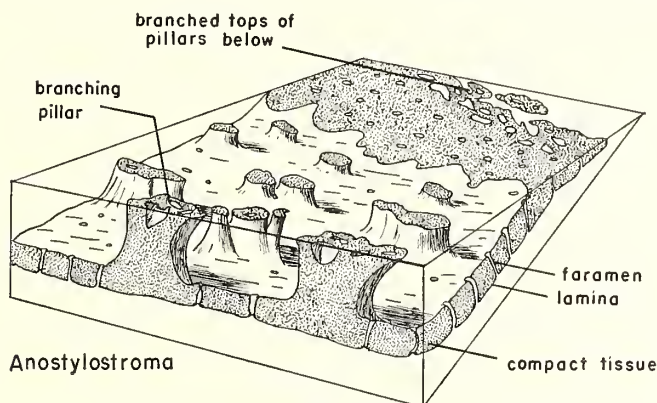
typified by *C. fastigiatum* Nicholson, in which the laminae are bent into chevron-like folds. He described the microstructure of the type species as being compact but marked by small dark dots that are conspicuous in tangential section. Nicholson's specimen (Nich. 240) from Estonia shows this texture well but the specimens of the same species from Shropshire show only compact, evenly speckled tissue. The dark dots are here interpreted as melanospheres developing out of originally compact tissue.

ANOSTYLOSTROMA Parks

Text-fig. 6

Type species: A. hamiltonense Parks

Coenosteum of regular, persistent laminae and short pillars. Laminae composed of a single layer of compact tissue that in some states of preservation appears to be transversely fibrous and in some to be transversely porous. Compact pillars confined to an interlaminar space and divide at the top either simply or into a network of tissue that spreads on to the underside of the laminae.



TEXT-FIG. 6. $\times 50$.

The holotype of *A. hamiltonense* (Pl. 15, fig. 3) in the Royal Ontario Museum has very dark tissue which stands out against the empty galleries lined with calcite crystals. The specimen shows some silicification. The specks in the tissue have not migrated into the galleries to any great extent. The laminae are a single layer of tissue which locally breaks up into a series of granules. At $\times 50$ the laminae seem to have fine, closely spaced canals running transversely through them but are not fibrous. The tissue of the paratype also lacks fibrosity. *Anostylostroma papillatum* Parks has tissue which is much the same but is locally flocculent and locally melanospheric. In tangential section the laminae seem to be penetrated by fine transverse pores.

The pillars of species of *Anostylostroma* from the central United States are commonly darker in colour than the laminae and locally their ends are embedded a short distance in the lighter laminar tissue (Pl. 14, fig. 4). In tangential section they appear as fibrous dots or vermiform bars that look like hairy caterpillars. Complexly branching pillars cut tangentially near the top form a network or irregular tangle of fibres. The fibrosity of the tissue is largely due to the alignment of specks but may also have a crystalline

basis. In *A. meshbergerense* (Galloway and St. Jean) the pillars have a dark axis from which the fibres spread out like those of a Mesozoic sphaeractinoid, but such microstructure is rare in *Anostylostroma*.

Many specimens of *Anostylostroma* show compact tissue only but the diverse development of transversely fibrous and porous microstructures is difficult to interpret. Some fibrosity seems to be secondary but the possibility that some reflects a primary microstructure cannot be eliminated. Transversely porous laminae, such as those of the type species, are not common in other species of the genus.

Rarely a specimen of *Anostylostroma* shows an axial light or dark zone in the laminae but these specimens are atypical and may be transitional to *Stictostroma*. The upwardly branching pillars and single-layered laminae distinguish *Anostylostroma* from *Stictostroma*.

HAMMATOSTROMA Stearn

Type species: H. albertense Stearn

Coenosteum composed of persistent laminae and incomplete pillars confined to a single interlaminar space. The laminae are a single layer of transversely fibrous speckled tissue. The pillars arise from the laminae and form a tangled irregular mass of strands between the laminae. The tissue of the pillars is speckled, not cellular.

In the original description of this genus (Stearn 1961) the laminae were described as transversely porous. Although variations in the density of the specks in the tissue suggest transverse porosity, the tissue in all the specimens I have seen is fibrous (Pl. 15, fig. 5). This fibrosity is not obvious in the tangled pillar tissue although it seems to be derived from the laminae. Yavorsky (1963, and personal communication) believes the tissue of both the laminae and the pillars of *Hammatostroma* to be porous. He points out that species assigned by Stearn to *Hammatostroma* largely on the basis of gross structure include some with compact tissue (*Clathrodictyon katavense* Yavorsky, and *C. tschussovense* Yavorsky) and one with porous tissue (*Stromatoporella undata* Yavorsky). He established the genus *Intexodictyon* to include largely Silurian but some Devonian species with compact tissue and irregular, incomplete, and almost cystose pillars.

I have been unable to examine Yavorsky's material but have seen specimens of *Intexodictyon* from the Silurian of Baffin Island, Arctic Canada. In structure these specimens are similar to *Hammatostroma* but their microstructure is not fibrous but compact and like that of *Clathrodictyon*. Nestor (1964) examined the original material of *C. katavense* and *C. tschussovense* and believed, as I do, that on the basis of microstructure they are best placed in *Hammatostroma*. He also believed that more evidence is needed before the range of *Intexodictyon* can be extended into the Devonian. These relationships suggest that similar gross structures were developed at different times in the history of the stromatoporoids, *Intexodictyon* from the compact *Clathrodictyon* in Silurian times, and *Hammatostroma* from the fibrous *Anostylostroma* in Devonian times.

DENDROSTROMA Lecompte

Type species: D. oculatum (Nicholson)

Coenosteum dendroid, columnar or branching, typically with an axial tabulated

tube. Other large tubes radiate from the axial one. Laminae thick, clearly differentiated from the pillars forming paraboloids around the axis of the coenosteum. Pillars confined to an interlaminar space, not superposed. Microstructure of both pillars and laminae compact, commonly transversely fibrous.

The Nicholson collection contains only one fasciculate specimen of *Dendrostroma oculatum* from which 31 sections were made. The other two specimens from Devon which were referred to this species are not conspecific. The tissue of Nicholson's type is speckled and much diffusion of specks into the galleries has taken place. The microstructure of the tissue is fibrous but like that of many compact stromatoporoids this fibrosity may be secondary. In a few places an axial light line appears in the tissue but this also seems to be secondary. In thicker parts of the sections the tissue appears to have tubules in it and is distinctly flocculent, not unlike that of *Stromatoporella* in some states of preservation. Lecompte (1951) suggested that the internal structure of this genus is comparable to that of *Stromatoporella*.

Galloway (Galloway and Ehlers 1960) described two species of *Dendrostroma* from Michigan. Of these I have seen only *D. fibrosum*, which as its name implies has a very fibrous tissue. Minute tubes parallel to the fibres seem to penetrate the tissue. Where not fibrous the tissue is flocculent.

Ripper (1937a) described some specimens of *D. oculatum* as being hemispherical rather than cylindrical. Such a coenosteum would be difficult to distinguish from that of *Stictostroma*.

STROMATOPORELLA Nicholson

Text-fig. 7

Type species: S. granulata Nicholson

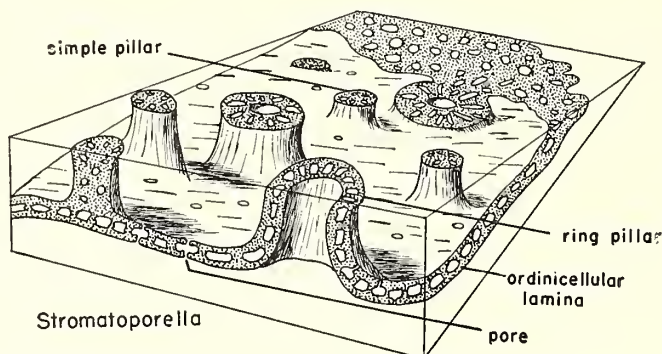
Coenosteum composed of well-defined laminae and short pillars confined to one interlaminar space. The laminae typically enclose a single series of subspherical cellules but one species at least shows more than one series. In some states of preservation the cellules may be expressed as a continuous axial clear zone in the lamina, in others as a series of pores crossing the lamina transversely. Some pillars are spool-shaped, others are formed by the upward inflection of the laminae into hollow cylinders which are cut as rings in tangential sections (ring pillars).

Two concepts of the structure of *Stromatoporella* can be found in descriptions of the genus. One concept set forth by Nicholson (1886) and followed by Lecompte (1951) emphasizes the relationship of the genus to *Stromatopora* and ignores or denies the existence of the distinctive ring pillars (but Nicholson in 1892 noted the distinctiveness of the ring pillars). The other, set forth by Parks (1936) and followed by Galloway and St. Jean (1957), emphasizes the relation of the genus to *Clathrodictyon* and recognizes the ring pillars as its essential feature. Yavorsky's views (1963) seem to fall between these extremes. Since the revision of Parks is based on the type species, it is accepted in this paper, as the diagnosis above indicates.

Nicholson (1886) described the microstructure of *Stromatoporella* as 'porous or finely tubulate'. Lecompte (1951) reviewed opinions on the microstructure and concluded that

it is no different from that of *Stromatopora*, that is, cellular or filled with small vacuities. Lecompte believed that the tubules which Nicholson described were not part of the original tissue but developed during preservation. He also stated (1951, p. 157) that a line of cellules in the laminae is not typical of the genus nor found in its type species.

However, vertical sections of the holotype of the type species (Nich. 329) show a line of cellules in the axis of the laminae, i.e. the laminae are ordinicellular (Pl. 15, figs. 6, 7). These chambers are not tubular but are equidimensional and appear in both tangential



TEXT-FIG. 7. $\times 50$.

and vertical sections as subcircular clear areas. The tissue in tangential section shows very fine specks (less than $1\ \mu$) which have diffused only slightly into the galleries, and small round clear cellules throughout. Where a ring pillar is formed by the upbending of a lamina, the cellules may be streaked out into radially directed short unbranched tubes. In parts of vertical sections of the tissue the microstructure of the laminae is preserved as a line of subspherical cellules, but locally the boundaries between the chambers break down and they merge into a central light zone. The spool-shaped pillars generally have a clotted or locally melanospheric texture and may contain some obscure cellules which are more prominent in tangential than in vertical sections.

Several other species in the Nicholson collection show ordinicellular structure. *Stromatoporella tuberculata* (Nicholson) shows an axial line of cellules which are replaced locally by transverse pores. The tissue of *S. selwyni* (Nicholson) approaches the microstructure of *Stromatopora*, for several zones of cellules forming a microreticulate structure are longitudinally aligned in the laminae and pillars (Pl. 15, fig. 8). In tangential section the laminae are also microreticulate. A specimen from the Eifel identified only as *Stromatoporella* sp. in the Nicholson collection (Nich. 371) also shows the cellules in the laminae and their blending locally into an axial light line. Several specimens of *Stromatoporella* in the St. Jean collection from Ontario which have not yet been described have the typical microstructure. In *S. columbusensis* Galloway and St. Jean the cellules are beautifully preserved, particularly where the galleries have been filled with sediment. The type specimen of *S. columbusensis* and others of *S. selwyni* suggest that the cellules opened into the gallery by a narrow pore on either side.

Ordinicellular microstructure is not preserved in many specimens or species (I have seen it in *S. granulata*, *S. selwyni*, *S. solitaria* (Nicholson), *S. tuberculata*, *S. columbusensis*, and *S. cellulosum* (Nicholson) [*Clathrodictyon cellulosum* auct.]). In the process of

preservation the microstructure has been changed by the destruction of the wall between the cellules so that they merge into a continuous axial light zone, or by the destruction of the wall between the cellule and the gallery producing transverse pores. Species which show such an axial light line (rarely dark by tissue reversal) include *S. eifeliensis* Nicholson, *S. kirki* Galloway and St. Jean, *S. eriensis* (Parks), and *S. perannulata* Galloway and St. Jean. The first of these has been assigned to *Clathrocoilona* and is discussed under that genus. The conversion of the cellules to transverse pores is particularly common in American species and can be seen in specimens of *S. cryptoannulata* Galloway and St. Jean, *S. huronesis* Parks, *S. parasolitaria* Galloway and St. Jean, and a manuscript species of St. Jean's.

Unfortunately many species which in their thick tissue and ring pillars seem to belong to *Stromatoporella* do not show any of these microstructures but may develop two others. In *S. arachnoidea* Nicholson the tissue of the pillars and laminae is thick and seems to be penetrated by fine light tubules about $5\ \mu$ in diameter (Pl. 16, fig. 2). In vertical section they seem to pass transversely through the laminae and in tangential section they wander irregularly in the tissue. They occur also in *S. morelandensis* Galloway and St. Jean, in *S. damnoniensis* Nicholson (which is here referred to *Stictostroma*), and to a lesser degree in *S. granulata*. The occurrence of these fine tubules in the tissue of some of these species (and *S. eifeliensis*) was the basis for Nicholson's conclusion that the tissue of the genus was typically finely tubulate.

Nicholson (1886, pl. 1, fig. 5) illustrated a set of branching tubules in the tissue of *S. granulata*. Neither Nicholson's catalogue nor the notations on the slides indicate specifically from which of the seven thin sections of this species the illustration was drawn. Slide 329a on which the notation 'pl. 1, fig. 4, 5, 15' appears is a tangential section and could not have included fig. 5. Nicholson's idealized drawing cannot be matched with any of the vertical thin sections but then his figures are all interpretative and commonly no part of the thin section exactly matches the drawing, even where the specific area from which the drawing was made has been indicated on the section. I was unable in the type slides to find a structure which corresponds to the axial canal with systematic branches illustrated by Nicholson. Apart from the elongation of the cellules, already described, where the ring pillars are formed, other species do not show fine tubular structures.

In most of these species the microstructure can be explained (Lecompte 1951) as formed during preservation and as associated with the clumping of fine specks into flocculent tissue. These thin irregular voids in the tissue are here called pseudotubules. Locally the pseudotubules look like shrinkage cracks in the tissue or appear to be related to transverse porosity. The pseudotubular microstructure is a variant of flocculent tissue and where the concentration of the specks has reached a further stage it may lead to melanospheric tissue. The development of melanospheres is common in species of *Stromatoporella* from the central United States. The occurrence of melanospheres and cellules in specimens of *Stromatoporella* has suggested to some that the tissue is closely related to that of *Stromatopora* and that various species of *Stromatoporella* evolved into species of *Parallelopore* and *Syringostroma* (Lecompte 1951). I believe that the single line of cellules opening into the galleries is a different type of microstructure to that shown by *Stromatopora*, where cellules are scattered throughout the amalgamate tissue. The cellular tissue characteristic of *Stromatopora*, *Syringostroma*, and *Parallelopore* was

widespread by Middle Silurian times but genera such as *Stictostroma* and *Stromatoporella* which have a single line of cellules are predominantly Middle Devonian genera.

The type species indicates that the essential features of the genus are the ring pillars and the ordinicellular laminae. I agree with Lecompte (1951) that tubules in the tissue are not characteristic of this genus and that secondary processes have given the tissue the appearance of having tubules in some specimens. There remain, however, some specimens in which the tubules are difficult to explain as secondary phenomena. The possibility that they may be the result of parasitic organisms such as infest modern corals and hydrozoans should be considered. I do not agree with Lecompte that the tissue has the overall cellularity of *Stromatopora* or that ring pillars are more characteristic of *Clathrodictyon* than of *Stromatoporella*. Galloway and St. Jean (1957) have also disagreed with Lecompte on this genus and have reassigned most of the species he described as *Stromatoporella* to the genera *Stictostroma* and *Clathrocoilona*. Of the species described by Lecompte *Stromatoporella decora*, *S. gracilis* and *S. pertabulata* have characters recognized as belonging to the genus here. Others have been assigned to *Clathrocoilona* (*S. saginata*, *S. obliterated*, and *S. spissa*) and other genera.

STICTOSTROMA Parks

Text-fig. 8

Type species: S. mamilliferum Galloway and St. Jean

Coenosteum composed of continuous laminae and pillars confined to an inter-laminar space. Laminae, where well preserved, enclose an axial line of cellules but in more common states of preservation have either an axial lighter zone or are transversely porous. Pillars simple, spool-shaped, composed of compact tissue and not systematically superposed.

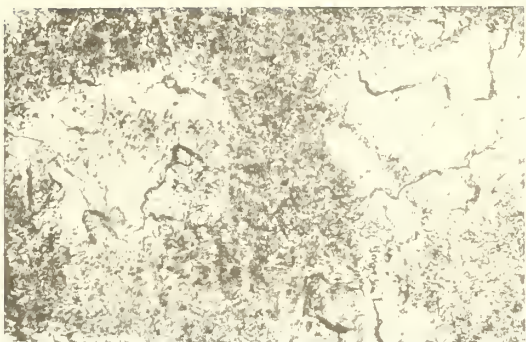
The validity of *Stictostroma* as a genus and the difficulties arising from Parks's (1936) unorthodox procedure of naming two type species have been reviewed by Lecompte

EXPLANATION OF PLATE 16

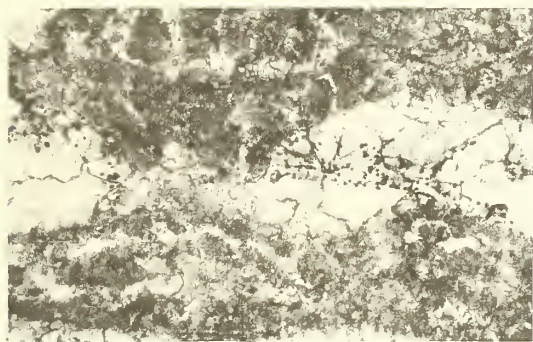
- Fig. 1. *Idiostroma caespitosum* Winchell (Univ. Michigan 32401a). Vertical section of holotype, $\times 50$, showing cellular nature of tissue. Middle Devonian, Petoskey, Michigan.
- Fig. 2. *Stromatoporella arachnoidea* Nicholson (Nich. 385b). Vertical section, $\times 100$, showing pseudotubules in flocculent tissue. Middle Devonian, Gerolstein, Germany.
- Fig. 3. *Clathrocoilona* [*Stromatoporella*] *eifeliensis* Nicholson (Nich. 342b). Vertical section, $\times 60$, showing tubulate tissue. Middle Devonian, Gerolstein, Germany.
- Fig. 4. *Stictostroma mamilliferum* Galloway and St. Jean (ROM 2151). Vertical section, $\times 50$, showing ordinicellular laminae, Middle Devonian, Gorrie, Ontario.
- Fig. 5. *Stictostroma* sp. (UNC 282-75). Vertical section, $\times 100$, showing transversely porous laminae. $2\frac{1}{2}$ miles E. of Arkona, Ontario.
- Fig. 6. *Gerronostroma elegans* Yavorsky (UNC 306-44). Vertical section of paratype, $\times 100$, showing transversely porous laminae. Middle Devonian, Kuznetsk Basin, Russia.
- Fig. 7. *Trupetostroma warreni* Parks (UNC 282-26). Vertical section, $\times 50$, showing suggestion of division of clear laminae into cellules. Middle Devonian, near Fort Norman, Northwest Territories, Canada.
- Fig. 8. *Anostylostroma maculosum* (Parks) (ROM 13,215a) (*Trupetostroma maculosum* of Parks). Vertical section, $\times 50$, showing melanospheres well developed in originally compact tissue. Upper Devonian, Charles City, Iowa.



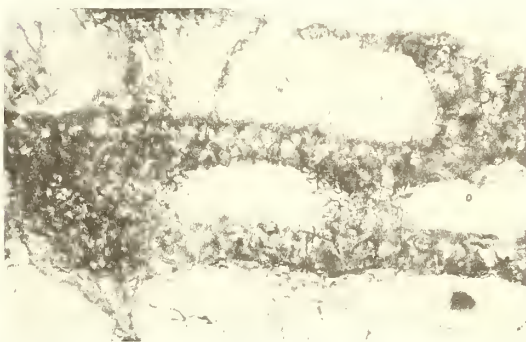
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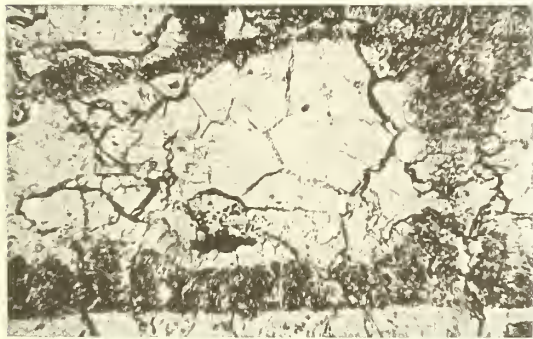
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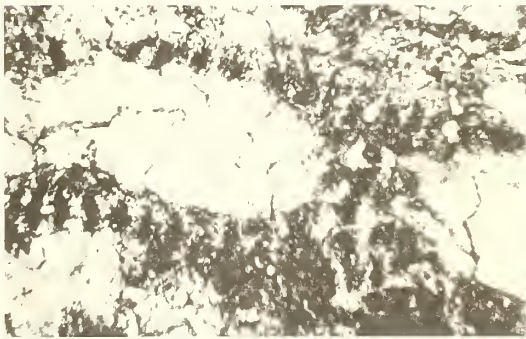
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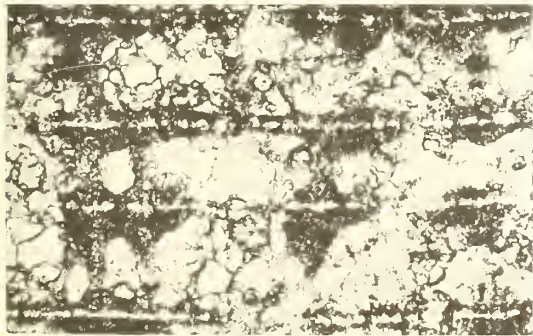
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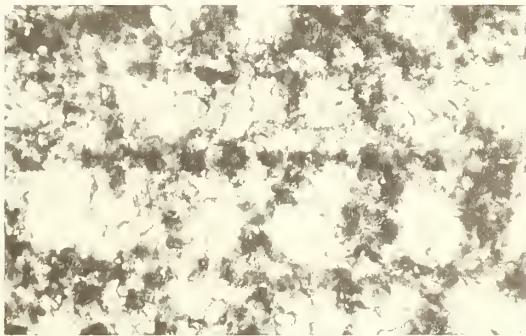
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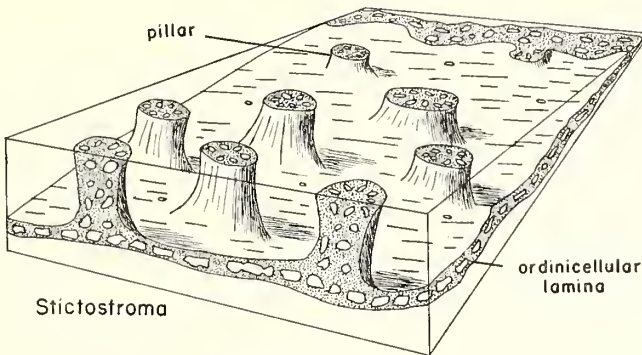
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8

(1951) and by Galloway and St. Jean (1957). The genus is a useful one for the reception of species that have the microstructure of *Stromatoporella* but do not have ring pillars. The microstructure of this genus has been the subject of a thorough study by St. Jean (1962) and therefore needs little further discussion here.

The holotype of *S. mamilliferum* (= *Stromatopora mamillata* Nicholson not Schmidt) was not located in Nicholson's collection. Topotype material in the University of North Carolina collection and at the Royal Ontario Museum from south-western Ontario, and particularly from Ashton's Quarry at Gorrie, shows the fine structure of the type species



TEXT-FIG. 8. $\times 50$.

described by St. Jean (Pl. 16, fig. 4). The laminae are relatively thin and have an axial line of small subspherical cellules (ordinicellular). In both vertical and tangential section these appear as subcircular clear areas in the speckled tissue. In the pillars the tissue also seems to be porous but this may be the result of the aggregation of the specks into melanospheres.

The laminar tissue seems to change in one of two directions during preservation. In some specimens the boundaries that separate the cellules from the galleries break down and a lamina with transverse pores passing from gallery to gallery is the result. This microstructure is also accompanied by the development of fibrosity in the tissue (Pl. 16, fig. 5). In other specimens the boundaries between the cells themselves break down and a continuous light zone appears along the axis of the lamina giving it a tripartite appearance. In *Stictostroma kayi* (Parks) and *S. elevatum* (Parks) some specimens show an axial dark, rather than light, zone and this has been described by St. Jean (1962) as due to the alignment of crystal boundaries. The dark zone of *S. elevatum* is too persistent to be explained as due to crystal boundaries and must be the filling of an axial void with bituminous matter (see p. 84).

Where the tissue is thick it may appear flocculent and, as in *Stromatoporella*, pseudotubules may appear between the concentrations of specks. Unfortunately many specimens with the gross structure of *Stictostroma* have laminae which show no distinctive microstructure but are a single layer of slightly fibrous tissue. In this state of preservation *Stictostroma* can be distinguished from *Anostylostroma* by the upwardly dividing pillars of the latter. Several of Nicholson's species of *Stromatoporella* are here referred to *Stictostroma* because they lack the ring pillars of the first genus. These include *Stromatoporella socialis* Nicholson, and *S. damnoniensis* Nicholson.

Galloway and St. Jean's (1957) assignment of a group of Lecompte's (1951) species of *Syringostroma* to *Stictostroma* is not justified. In this group tangential sections show a network which cannot be reconciled with the structure of the type species of *Stictostroma*. I agree that these species are not *Syringostroma* but would provisionally assign them to such genera as *Atelodictyon* (*Syringostroma microfibrosum* Lecompte), *Ferestromatopora* (*S. percaniculatum* Lecompte), and possibly *Stromatopora* (*S. minutitextum* Lecompte) pending revision.

CLATHROCOILONA Yavorsky

Type species: C. abeona Yavorsky

Coenosteum composed of thick laminae and pillars which enclose small rounded galleries. Laminae laterally persistent, divided by a narrow axial light zone into three layers. Pillars confined to a single interlaminar space, spool-like, not commonly superposed. Galleries small and rounded, not as high as the laminae are wide. Tissue of laminae and pillars compact.

In his original definition of this species Yavorsky (1931) emphasized the restriction of the galleries to round openings and the compactness of the tissue. On the basis of Yavorsky's illustrations of the type species in tangential section and the examination of a topotype, Galloway and St. Jean (1957) determined that the genus should be interpreted as maculate (cellular of this paper). They described four species from Indiana including one specimen identified with the type species. I have, through the courtesy of Dr. St. Jean, examined these and would describe the tissue as speckled, fibrous, and to a minor extent flocculent, but none of the species is distinctly melanospheric (darkly maculate) or cellular. The tissue in all is thick and the laminae are marked by a clear line. Galloway and St. Jean (1957) assigned thirteen species to *Clathrocoilona*, four of which were described by Lecompte (1951) as *Stromatoporella*. These four species were described by Lecompte as having traces of cellular tissue but in some (e.g. *S. saginata* Lecompte) the tissue is not clear enough to make the determination of microstructure positive. Of these I have been able to examine only the specimens in the Nicholson collection which Lecompte referred to his *Stromatoporella saginata* (Nich. 362) and *S. crassitexta* (Nich. 356). In the first no cellular structure occurs, but in the second, parts of the tissue are cellular and Lecompte noted that the Belgian specimens show aligned cellules.

The interpretation of this genus can be made only on the basis of Yavorsky's original descriptions, repeated in 1955 (p. 38) and his assertion that a second species described by him (*Clathrocoilona solidulum* Yavorsky 1955) is also compact. As so described, the genus comprises species much like *Stictostroma* in which the tissue is so thickened as to restrict the galleries. A convenient line between these two genera can be drawn where the thickness of the laminae reaches the height of the galleries. With its spool-shaped pillars and tripartite laminae *Clathrocoilona* is out of place amid genera with cellular tissue and generally amalgamate structure, but is naturally related to genera with compact tissue. Most of Lecompte's species assigned by Galloway and St. Jean to *Clathrocoilona* cannot be accepted in the genus as originally described because they have cellular tissue; *S. crassitexta* Lecompte, and *S. irregularis* Lecompte may be species of *Stromatopora*. Such species as *Stromatoporella spissa* Lecompte, *S. saginata* Lecompte, and *S.*

obliterata Lecompte can be assigned to this genus with Yavorsky's and Galloway and St. Jean's specimens of *Clathrocoilona*.

The position of *Stromatoporella eifeliensis* Nicholson, which Galloway and St. Jean (1957) referred to *Clathrocoilona*, remains enigmatic as it is one of the very few species which have tortuous, irregular, clear tubules (20–30 μ wide) penetrating the thick tissue (Pl. 16, fig. 3). Some of the specimens included by Nicholson in this species are not con-specific with the type (see also Lecompte 1951, pp. 175–6). The microstructure is not cellular nor simply compact but the species may be retained in *Clathrocoilona* until its peculiar microstructure is found to be more widespread.

ACTINODICTYON Parks

Type species: A. canadense Parks

Coenosteum cylindrical in all known species, composed of irregularly crumpled laminae and through-going pillars. The laminae resemble dissepiments and are inflected irregularly up and down so that they are impersistent and abut against each other as in some species of *Clathrodictyon*. Pillars thick, irregular in cross-section. Laminae and pillars of compact tissue.

Although Galloway and St. Jean (1957) described the tissue of the type species as 'obscurely maculate', Parks (1909) insisted that the type and genus are characterized by 'dense' (i.e. compact) tissue. He correctly pointed out its resemblance to *Clathrodictyon* and referred to the horizontal elements as laminae, although later writers (Galloway and St. Jean 1957; Flügel 1958) have referred to them as cysts. Examination of the fragments of the type of *A. canadense* at the Royal Ontario Museum convinced me that Parks's interpretation is correct and that the relationship of the genus to *Clathrodictyon* is close.

Flügel (1958) suggested that of Parks's four species, *A. neptuni* is the same as *A. canadense*, *A. keelei* Parks is a *Clathrodictyon*, and *A. lowi* Parks is a valid species. Examination of the slides of these species showed that the tissue of all is compact. *A. keelei* is more like an *Actinostroma* than a *Clathrodictyon* but in any case does not belong to this genus.

Nestor (1964) independently reached the conclusion that the microstructure of *Actinodictyon* is compact and assigned *Actinostroma intertextum suevicum* Nicholson, a compact species, to this genus as *Actinodictyon suevicum* (Nicholson).

PSEUDOACTINODICTYON Flügel

Text-fig. 9

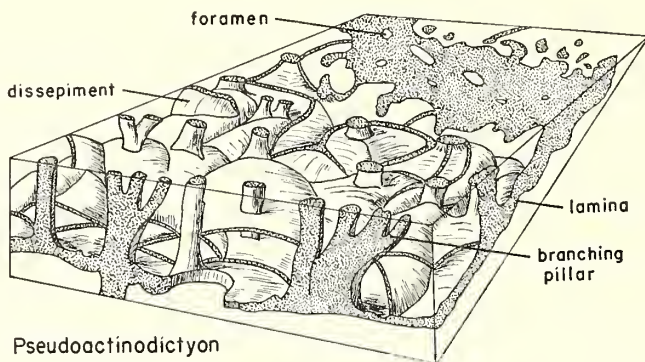
Type species: P. juxi Flügel

Coenosteum composed of persistent thin laminae and short rod-like pillars, some of which are confined to an interlaminar space, others cross several laminae. High interlaminar spaces crowded with large overlapping dissepiments. Laminae a single layer of compact tissue with isolated foramina. Pillars compact or flocculent.

Flügel (1958) established this genus for the type species, *P. juxi*, and *P. vagans* (Parks) to separate these Devonian species with laminae from Silurian species without laminae

which Parks included together in *Actinodictyon*. I examined the type specimens of *P. juxi* in the Senckenberg Museum, Frankfurt, and those of *P. vagans* in the Royal Ontario Museum, Toronto.

Although Flügel (1958) described the tissue of *P. juxi* as 'gefleckt' (= maculate) I believe that it is better described as flocculent or compact. The tissue of the laminae is a single layer of flocculent tissue with widely scattered foramina that may be covered with a convex plate. The pillars are round in cross-section and appear to be compact.



TEXT-FIG. 9. $\times 50$.

Many of them are short and confined to an interlamina space but some penetrate several laminae. The shorter ones divide conspicuously at the top, much like those of *Anostylostroma*, and may spread along the under surface of the laminae producing a layer of vacuolate tissue.

Pseudoactinodictyon vagans (Parks) (Pl. 15, fig. 4) has a similar structure of widely spaced laminae and many convex dissepiments. Some of the pillars are long, others short. Some divide upwards as in *P. juxi*. The tissue of the laminae, pillars, and dissepiments is all similar and coarsely speckled. Where thick it seems to be composed of dark granules about $10\ \mu$ across. The tissue is not cellular nor markedly melanospheric but some vacuoles may appear in the pillars.

Galloway and St. Jean (1957) described a specimen of *Pseudoactinodictyon vagans* from Indiana and redescribed Parks's type material. I disagree with their interpretation of the tissues of the type as maculate (in the sense that it is similar to that of *Stromatopora*). Neither the gross structure nor microstructure of this genus justifies its classification with the family Stromatoporidae. Flügel (1958) suggested that the specimen described by Galloway and St. Jean from Indiana as *Actinodictyon vagans* is a new species. Its tissue is coarsely speckled and locally the specks are aggregated into dark masses about $7\ \mu$ across.

Pseudoactinodictyon norrisi Stearn was described (Stearn 1962) before I had seen the type species and when I understood the tissue of the genus to be 'maculate'. It is not congeneric with *P. juxi* as its tissue is cellular and laminae poorly defined. It is now referred to *Ferestromatopora*. *P. athabaskense* Stearn has flocculent tissue and is closer to the type species.

Species described by Lecompte (1951) and Le Maître (1934, 1949) under *Actinostroma* are further discussed by Flügel (1958).

GERRONOSTROMA Yavorsky

Type species: G. elegans Yavorsky

Coenosteum composed of well-defined compact pillars and laminae. Laminae persistent and transversely porous. Pillars spool-shaped, composed of porous tissue and conspicuously superposed from one interlaminar space to the next.

The genus was proposed by Yavorsky (1931) for the reception of species like *Actinostroma* which do not show the radial arms and 'hexactinellid network' of that genus. *Gerronostroma* is much more closely allied to *Stictostroma* and differs essentially only in the superposition of the pillars. Yavorsky (1931, p. 6) described the microstructure of the tissue as compact or massive; however, sections of a paratype in the collections at the University of North Carolina (UNC 306-43-44) show that the laminae are transversely porous in much the same way as some specimens of *Stictostroma* and *Stromatoporella*, and that this porous structure continues into the pillars (Galloway and St. Jean 1957, p. 152; and Pl. 16, fig. 6). As in *Stictostroma* these pores do not show in all states of preservation and in most places even in the paratype the tissue appears to be transversely fibrous owing to the alignment of the specks.

The genus has been used extensively only by Russian palaeontologists. Galloway and St. Jean (1957) established two new species of this genus and assigned *Stictostroma insolitum* Parks to it. *G. plectile* Galloway and St. Jean is much like *Anostylostroma* and might be included in that genus. Both *G. excellense* and *G. insolitum* show curious circular structures in tangential section which are similar to, if not identical with, the ring pillars in *Stromatoporella*. Both species have other features that make assignment to *Stromatoporella* difficult. The laminae of these species seem flocculent or transversely fibrous and only in isolated parts of *G. cf. insolitum* is there a suggestion of transverse porosity. These species seem therefore to be transitional to *Stromatoporella*.

In *G. excellense* an axial light line may occur in the laminae suggesting that the transverse porosity may have originated in a line of cellules in the axis of the laminae as in *Stictostroma*. Although no direct evidence of such a structure has yet been described, the analogy with the structure of *Stictostroma* and *Stromatoporella* is suggestive.

Several specimens which Nicholson assigned to *Actinostroma* are placed here in *Gerronostroma*. *Actinostroma matutinum* Nicholson has no suggestion of radial arms. Although the preservation of the specimens is poor and the possibility that it is a *Trupetostroma* cannot be eliminated, the species is here provisionally assigned to *Gerronostroma*. Two specimens from Gerolstein (Nich. 458, 460) grouped by Nicholson in a manuscript species represent different species of *Gerronostroma*. The specimen from Gerolstein referred to by Ripper (1937b, p. 31, Sedgwick Mus. A 4651) as *Actinostroma stellulatum* is a *Gerronostroma*, and specimen 174 of Nicholson's collection also referred to this species belongs to this genus too. *A. contortum* Ripper and *A. stellulatum distans* Ripper are both better placed in *Gerronostroma*. The former has been assigned by Galloway and St. Jean (1957) to *Anostylostroma* and renamed *A. buchanense* to eliminate homonymity with *Actinostroma contortum* Gorsky (Flügel 1958, p. 183).

Although *Gerronostroma* is close to *Trupetostroma*, its laminae do not normally show

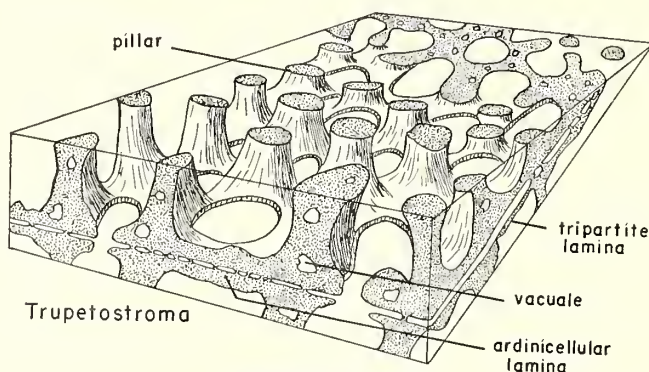
three layers nor the large circular foramina of this genus. Both these features seem to be due to the extension of the pillar tissue on to the laminae in *Trupetostroma*.

TRUPETOSTROMA Parks

Text-fig. 10

Type species: T. warreni Parks

Coenosteum composed of persistent three-layered laminae consisting of an axial light or dark zone covered irregularly with thicker tissue, and short spool-shaped pillars. Pillars superposed from one interlamina space to the next, forming with the laminae a grid in vertical section. Laminae pierced by large circular foramina between the pillars or reduced to a network. Tissue of pillars and outer zones of laminae compact but may contain widely separated vacuities.

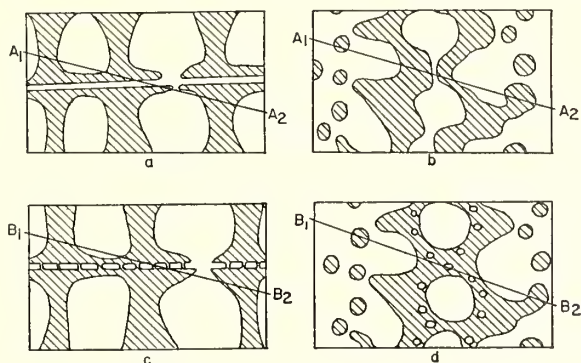


TEXT-FIG. 10. $\times 50$.

The type species has been described by Parks (1936), Galloway and St. Jean (1957), Galloway (1960), and Stearn (1963). The three-fold nature of the laminae and the superposition of the spool-shaped pillars are conspicuous elements of its structure.

Slides of the holotype of *T. warreni* at the Royal Ontario Museum (ROM 13197) show that the pillars are compact in microstructure and very finely and evenly speckled (Pl. 17, figs. 1, 2). Little or no migration of specks has taken place at the edges of the tissue into the galleries. Vacuoles are inconspicuous in vertical sections but those present seem to be randomly distributed and are not concentrated on the periphery of the pillars. In several places they seem to be voids produced by the joining of adjacent pillars at the bottom and top. Locally they appear in the tissue coating the clear axial zone of the laminae. They are large ($50\ \mu$), considerably larger than the cells of *Stromatopora*. The nature of the axial clear zone of the laminae is obscure. Although Parks (1936) described the zone as having a continuous independent existence across the section, it disappears completely in the area between the pillars and is defined only where bordered by the darker tissue of the pillars. The type vertical sections do not show any structure within this clear zone but Galloway's (1960) specimen (UNC 282-26, which is not a topotype as implied in Galloway 1957, p. 464, and Galloway and St. Jean 1957, p. 160) suggests but does not show clearly that the zone is divided into cellules by cross partitions much as in *Stictostroma* (Pl. 16, fig. 7).

Tangential sections of the type are difficult to reconcile with vertical sections. Between the laminae the pillars are round and may contain vacuoles. Towards the laminae they are arranged in circles and coalesce at their bases into a network which encloses circular foramina. The breaking of the network into discrete pillars marks the other side of the lamina. The clear axial zone of the laminae, so conspicuous in vertical sections, cannot be identified in tangential sections. If such a continuous planar open space existed in the structure it should be represented by a clear line between the networks formed by the coalescence of the pillars above and below (see text-fig. 11). Around the edges of the foramina in tangential sections of the type is a series of small round vacuities (Pl. 17, fig. 2). These have been interpreted by Galloway and St. Jean (1957) and by Parks (1936)



TEXT-FIG. 11. Alternative interpretations of *Trupetostroma* in vertical and tangential sections. In *a* and *b* the clear zone in the lamina is assumed to be a planar open space. Such an assumption requires a continuous clear zone in the centre of the lamina in tangential section (*b*). In *c* and *d* the clear zone is assumed to be made up of a line of cells. The tangential expression of such a microstructure is represented in *d* and is closer to reality. A_1A_2 and B_1B_2 are corresponding lines in vertical and tangential sections.

as vacuoles in the tissue that has spread out from the pillars, but they are not conspicuous in this position in vertical section. They could be interpreted as cross-sections of a sheet of cells that occupies the axial light zone of the laminae.

If the laminae were originally ordinicellular as suggested above, the partitions between the cellules must have been very fine for they are rarely preserved. In other species of *Trupetostroma* the position of the axis of the lamina is commonly infiltrated by bituminous matter and a dark line which traverses the foramina as well as the pillars results.

The type species indicates that the characters fundamental to the recognition of the genus are as follows: (1) Laminae that are three-layered, vacuolate or cellular and traversed by large foramina which may reduce them to a network; (2) short, spool-shaped, superposed pillars; (3) compact, vacuolate tissue.

Parks's assignment of a diverse group of species to this genus has hindered an understanding of its limits. The following species, other than the type, were placed by Parks in *Trupetostroma*:

Trupetostroma iowaense Parks. Prominent marginal vacuoles and no laminae, only dissepiments. Closer to *Hermatostroma* than to *Trupetostroma*.

Trupetostroma coralvillense (Thomas). Not like the type species; superposition of pillars poor; possibly a *Stictostroma*. Assigned by Galloway and St. Jean (1957) to *Stromatopora* but has flocculent tissue.

Trupetostroma planulata (Hall and Whitfield). This species has been variously interpreted as *Cannopora* (Hall and Whitfield 1873), *Syringostroma* (Fenton 1920), and *Parallelopore* (Galloway and St. Jean 1957). The figure of Parks (1936, pl. 9, fig. 3) is not a good representation of his thin section, which shows little organized structure. Other representatives of this species examined suggest that it is best placed in *Parallelopore*.

Trupetostroma maculosum Parks. Parks's specimen is a highly melanospheric form of *Auostylostroma* (Pl. 16, fig. 8).

Trupetostroma incrustans (Hall and Whitfield). Poorly organized structure, probably *Clathrocoelona*.

Trupetostroma erraticum (Hall and Whitfield). Poorly organized structure, probably *Clathrocoelona*.

Trupetostroma solidulum (Hall and Whitfield). Poorly organized structure. Parks's specimen looks much like *Parallelopore planulata*.

Of these species none is conspecific with the type species as described here. Parks also suggested (1936, pp. 54, 55) that *Parallelopore dartingtonensis* (Carter) might be assigned to *Trupetostroma*. This difficult species is not a typical *Parallelopore* but because all the specimens come from the deformed rocks of Devon and the microstructure is obscure, its generic assignment is doubtful. The types described by Carter have not been located but topotypes are in the Nicholson collection and a specimen from the Pit Park Quarry, Dartington (Nich. 126, P 5746) is here designated the lectotype. It is the specimen illustrated by Nicholson (1891, pl. 24, fig. 15, and pl. 25, fig. 1). It is not a typical *Trupetostroma* for in tangential section the pillars are not circular at any level of the coenosteum but anastomose irregularly into an irregular network. The tissue is finely speckled and has spread into the galleries, precluding the determination of whether it was originally cellular, vacuolate, or compact. Until better material is available the assignment of this species will be in doubt. Some specimens labelled *P. dartingtonensis* in the collection from Teignmouth (e.g. Nich. 129, 130) are definitely *Trupetostroma* but they are not conspecific with the Dartington material. The type specimen of *Parallelopore dartingtonensis fillitexta* Nicholson (Nich. 137) is better preserved than *P. dartingtonensis* but the tissue has been recrystallized and is now uniformly speckled. The specimen is not a *Trupetostroma* but shows close affinities to the genus *Pseudoactinodictyon*.

The concept of *Trupetostroma* discussed above is that formulated by Parks and accepted by Galloway and St. Jean (1957) but Lecompte (1952) interpreted the genus in another light. From an illustration by Parks (1936, pl. 10, fig. 2) he concluded that the

EXPLANATION OF PLATE 17

Figs. 1, 2. *Trupetostroma warreni* Parks (ROM 13,197). 1, Vertical section of holotype, $\times 50$, showing compact tissue with few vacuoles. 2, Tangential section of holotype, $\times 50$, showing compact tissue of round pillars at left and lamina at right. Devonian, Great Slave Lake, Canada.

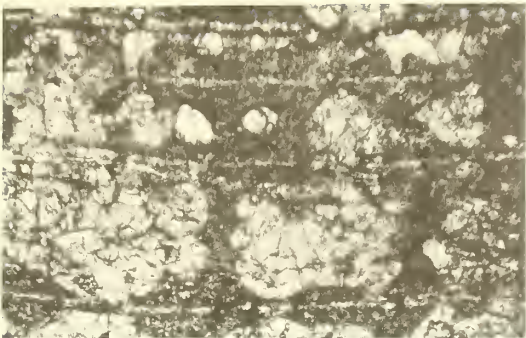
Fig. 3. *Idiostroma roemeri* Nicholson (Nich. 406c). Cross-section of holotype, $\times 60$, showing compact laminae and pillars with peripheral membranes. Middle Devonian, Hebborn, Germany.

Figs. 4, 5. *Hermatostroma schliiteri* Nicholson (Nich. 386h and 386a). Vertical and tangential sections of holotype, $\times 60$, showing compact tissue and marginal membranes. Middle Devonian, Hebborn, Germany.

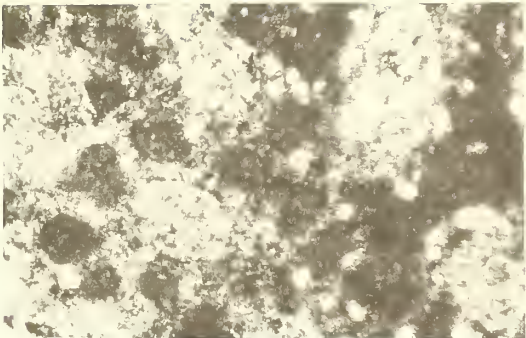
Fig. 6. *Stromatopora concentrica colliculata* Nicholson (Nich. 18). Tangential section, $\times 100$, showing melanospheric tissue. Middle Devonian, Teignmouth, Devon.

Fig. 7. *Stromatopora divergens* Galloway and St. Jean (UNC 294-30). Vertical section of holotype, $\times 100$, showing dark microlaminae and melanospheric tissue. Middle Devonian, 5 miles E. of Logansport, Indiana.

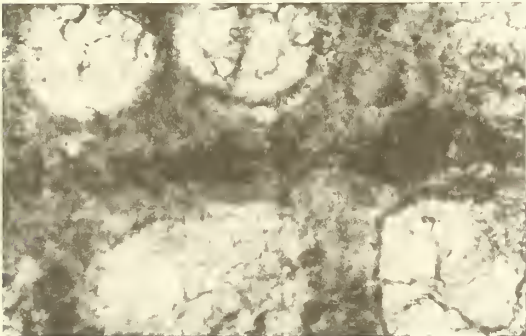
Fig. 8. *Hermatostroma beuthi* (Bargatzky) (Nich. 66). Tangential section, $\times 50$, showing melanospheric tissue bordered by a thin membrane. Middle Devonian, Hebborn, Germany.



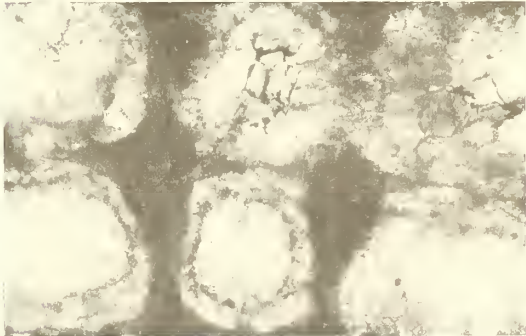
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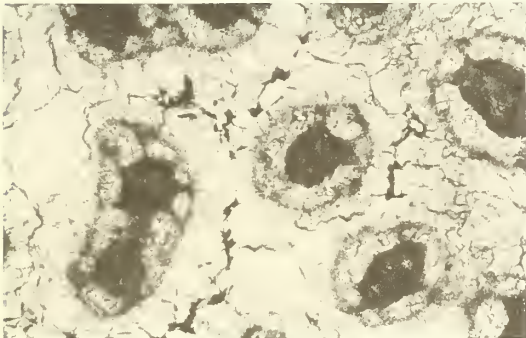
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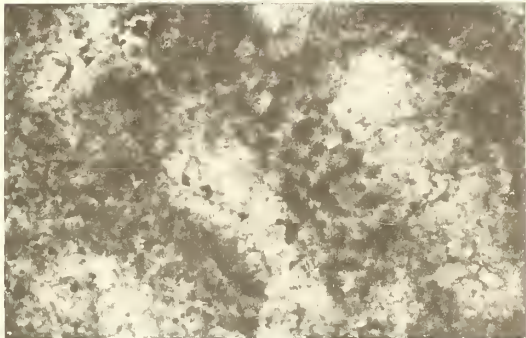
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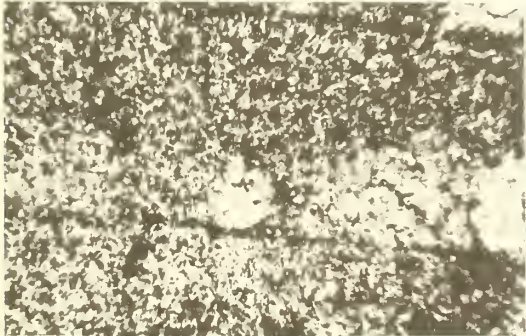
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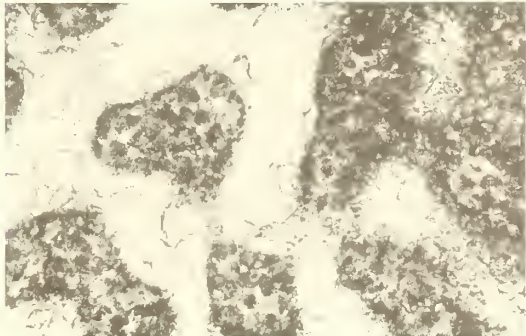
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tissue of *Trupetostroma* is cellular, like that of *Stromatopora*, and that the cellules are concentrated on the margins of the pillars. No other investigator having examined the type material has described it as cellular, and Parks himself emphasized (1936, pp. 56, 57) that the microstructure of both *T. warreni* and *T. iowaensis* was not cellular or spongy. The species of *Trupetostroma* described by Lecompte as having uniformly cellular tissue are better removed to *Stromatopora* (*T. sublamellatum* Lecompte, *T. rnedemanni* Lecompte) or to *Parallelopore* (*T. tenuilamellatum* Lecompte). A large group of Lecompte's species assigned to *Trupetostroma* (*T. cimacensis*, *T. porosum*, *T. mailleuxi*, *T. crassum*, *T. thomasi arduennensis*) show a progressive development of marginal membranes on the pillars, a microstructure peculiar to *Hermatostroma*. The interpretation of the vacuoles of the type species as the initial stage in the development of such membranes is not justified. The structure and microstructure of these species is closer to that of *Hermatostroma* than to that of *Trupetostroma*, but some may represent transitional forms between the two genera. Lecompte's species that are here retained in *Trupetostroma* (*T. bassleri*, *T. laceratum*, *T. pingue*, *T. thomasi*) have features closer to the type. In these species the pillars are circular in section for only a short distance between the laminae and merge in the laminae into a network of amalgamate structure.

Other species that have been described as, or referred to *Trupetostroma* and do not have compact tissue or pillars of circular cross-section between the laminae should be assigned to *Stromatopora*. They include such species as *T. macrostylum* Le Maître and *T. schelomense* Yavorsky.

Several problems concerning the interpretation of *Trupetostroma* remain. One of these is the difficulty of distinguishing vacuolate from cellular microstructure. Although they are here accepted as different microstructures, this does not imply that one may not grade into the other or that one did not give rise to the other. The possibility that cellular structure arose in several lineages of stromatoporoids or even repeatedly should not be overlooked. Determination of microstructure may be difficult in poorly preserved specimens that do not show the vacuoles, and the separation of such genera as *Trupetostroma*, *Gerronostroma*, and *Hermatostroma* may present problems.

IDIOSTROMA Winchell

Type species: I. caespitosum Winchell

Coenosteum dendroid, columnar, or fasciculate, typically with an axial branching tabulate canal. Laminae and pillars well defined in the peripheral zone. Laminae composed of a thin dark axial zone clothed in lighter tissue and arch upward from periphery in paraboloids. Pillars superposed to continuous, diverge upwards keeping perpendicular to the laminae, forming with them a network with open galleries. Microstructure of the tissue is compact but may have vacuoles.

For many years the interpretation of *Idiostroma* was based on the descriptions by Nicholson of *Idiostroma roemeri* Nicholson because the type species, *Idiostroma caespitosum* Winchell, had not been adequately described. The laminae and pillars of *I. roemeri* are equally developed and composed of compact tissue in which marginal membranes and vesicles appear on some specimens. Nicholson (1886) described the microstructure of *Idiostroma* as coarsely porous but did not note the peripheral membranes in *I. roemeri* from Hebborn, Germany. The holotype of this species does

not show a conspicuous internal porosity, only the marginal vesicles (Pl. 17, fig. 3). Nicholson's views on the coarse porosity may have been owing to his inclusion in the genus of *Parallelopora goldfussi* (1886, p. 100), which is coarsely porous, for neither *I. roemeri* nor *I. occulatum* Nicholson (now *Dendrostroma*) are porous. On the basis of his examination of *I. roemeri*, Lecompte (1952) believed that marginal vesicles on the tissue are characteristic of the genus but because he recognized striations like those of *Stachyodes* in the tissue of two species, he preferred not to base the genus on microstructure but on gross structure. These two species, one of which had been first described as *Stachyodes* (*S. verticellata irregularis* Heinrich), are both placed back in *Stachyodes* by Galloway and Ehlers (1960).

The redescription of Winchell's types of *Idiostroma caespitosum* by Galloway and Ehlers (1960) has opened the way to a fuller understanding of the genus. Through the courtesy of Dr. E. C. Stumm I was able to examine slide W2-18 (Univ. of Michigan 32401a) cut by Galloway from Winchell's type (Pl. 16, fig. 1). The tissue is not conspicuously speckled but seems to be distinguished from the gallery filling largely on the basis of its finer crystallinity. It is full of subspherical voids. Galloway and Ehlers (1960) described the tissue as 'not maculate but it is of variable compactness and is vacuolate, light, dark and mottled, with abundant dust particles' (p. 65). However, in the subsequent discussion of the similarity of *I. caespitosum* to *Stachyodes gracilis* Lecompte and *S. paralleloporoides* Lecompte (pp. 65, 102) they imply that the pores are maculae. The tissue is not like that of *Idiostroma roemeri* which is centrally compact and contains peripheral vacuoles. The tissue of *I. caespitosum* is similar to that of *Stromatopora* and could be described as cellular. In places vague suggestions of the striated microstructure of *Stachyodes* occur in the tissue, as noted by several writers. Ripper (1937a) and Lecompte (1952) have recognized that the genus embraces a variety of structures in a dendroid form which might be placed in other genera. Lecompte separated *I. occulatum* Nicholson in the new genus *Dendrostroma* and noted that in marginal vesicles other species of *Idiostroma* resemble *Hermatostroma* and *Trupetostroma*. Ripper (1937a) described *Idiostroma* as being massive in some species, but this applies only to her description of *I. occulatum*, which is further discussed under *Dendrostroma*.

If the form of the coenosteum is ignored, most of the species of *Idiostroma* may be distributed to other genera, principally *Trupetostroma*. As the laminae and cellular tissue of the type species make its assignment to any other genus difficult, the genus is retained. The following reassignment of species of *Idiostroma* is suggested:

<i>Idiostroma roemeri</i> Nicholson	— <i>Hermatostroma</i>
<i>Idiostroma occulatum</i> Nicholson	— <i>Dendrostroma</i>
<i>Idiostroma crassum</i> Lecompte	— <i>Stachyodes</i>
<i>Idiostroma fililamellatum</i> Lecompte	— <i>Trupetostroma</i>
<i>Idiostroma mclearnii</i> Stearn	— <i>Trupetostroma</i> .

HERMATOSTROMA Nicholson

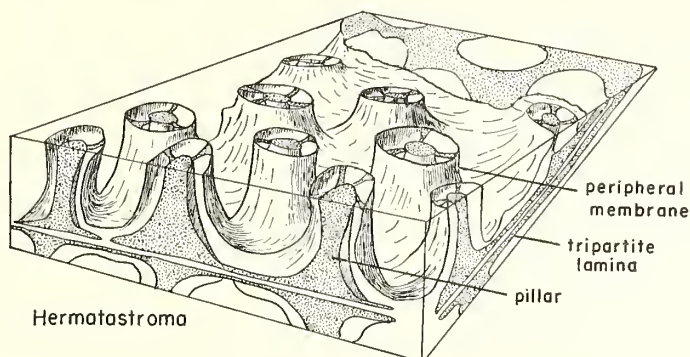
Text-fig. 12

Type species: *H. schlüteri* Nicholson

Coenosteum composed of distinct pillars and laminae forming a grid in vertical section. Laminae have continuous axial microlamina and a lighter, discontinuous

coating of tissue spreading from pillars. Pillars spool-shaped, circular in cross-section, interrupted by laminae but accurately superposed, composed of compact tissue in the type species. Both pillars and laminae are covered by peripheral membranes which are held a short distance away from them by small processes, or by a series of marginal vesicles or vacuoles along the edges of the galleries.

The type species, *H. schlüteri*, is represented in the Nicholson collection by a single specimen whose tissue is intensely but unevenly pigmented. Nicholson (1892, p. 217) misinterpreted this dark staining as opaque matter injected into axial canals of the laminae and pillars, but this view was discussed at length and rejected by Lecompte



TEXT-FIG. 12. $\times 50$.

(1952). The type specimen shows well-defined laminae and pillars, dark in colour and certainly compact (Pl. 17, figs. 4, 5). I found no evidence for the statement by Galloway and St. Jean (1957, p. 219) that 'the laminae and pillar tissues are obscurely but coarsely maculate'. Neither did Nicholson (1892) nor Lecompte (1952). In tangential section the pillars show no internal vacuities, although well preserved, but distribution of the opaque matter is irregular in the laminae as shown by Nicholson (1886, pl. 3, fig. 1). This is not typical nor evidence that the tissue is cellular. Near the laminae the processes to the peripheral membranes seem more numerous and in tangential section the peripheral space seem to break up into cellules. The laminae are partly formed by the periodic thickening and coalescing of neighbouring pillars to form a network, but this thickening tissue is based on a thin microlamina that appears in vertical section to be continuous. This gross structure is almost identical with that of *Trupetostroma*. In some species of *Hermatostroma* the structural elements are coated by vesicles but in the type species this marginal zone is not composed of overlapping cysts but is a continuous thin membrane that tangential sections show is held off the pillars by small radial processes (Pl. 17, fig. 5).

The principal problems in the interpretation of this genus are (1) the inclusion of cellular and compact species in a single genus, and (2) the relationship of the marginal membranes to the vacuoles of *Trupetostroma*.

Cellular and Compact Species. Nicholson described the microstructure of the type species of *Hermatostroma* as compact but that of *H. episcopale*, his other species, as porous. With the inclusion of the latter he enlarged the limits of the genus to include species with

porous tissue. The preservation of the type species of *H. episcopale* is typical of the stromatoporoids from Devon and neither the marginal membranes nor the microstructure of the pillars is satisfactorily preserved. Characteristically tangential sections of this species include a few opaque dots of doubtful significance. One of the best preserved specimens (Nich. 392) shows flocculent tissue with melanospheres. No fundamental conclusions on the structure of the genus can be drawn from these specimens.

Galloway and St. Jean's (1957) statement that the genus is coarsely maculate may have been influenced by their description of *Hermatostroma logansportense* Galloway and St. Jean. Its lack of continuous laminae and well-developed marginal membranes indicates that this species is not a typical *Hermatostroma*. In addition the microstructure of the type specimen (UNC 279-2, 3) did not seem to me to be conspicuously maculate (melanospheric or cellular) but is so described by the authors. Galloway and Ehlers (1960) also described a specimen of *H. episcopale* from Michigan but this does not show the marginal membranes and the tissue is flocculent rather than melanospheric or cellular.

Although these species do not demonstrate the association of both cellular and compact tissues with the gross structure of *Hermatostroma*, other evidence indicates that this association exists. The type specimens of *Hermatostroma beuthii* (Bargatzky) (Nich. 63; Bargatzky specimens were also examined) have the gross structure of *Hermatostroma*, but none of the slides shows cellular tissue or the marginal membranes distinctly. However, a topotype specimen (Nich. 66) which has the structure of the type shows both well (Pl. 17, fig. 8). Other specimens that Nicholson assigned to this species are a diverse group, some of which belong to *Stromatopora* (Lecompte 1952). Of the species of *Hermatostroma* described by Lecompte some are cellular throughout and some have only marginal cellules. *H. perseptatum* has well-developed peripheral membranes and internally apparently compact tissue. *H. pustulosum* has a line of cellules on the edges of the pillars also. *H. parksi* has cellules largely at the edges of the pillars but Lecompte (1952) states that the whole tissue is in places cellular. Some of the species transferred here from *Trupetostroma* to *Hermatostroma* also show cellular microstructure throughout the tissue (e.g. *T. porosum*). If peripheral membranes, marginal vesicles and vacuoles are taken as generic characters for *Hermatostroma* then the genus contains two groups of species, one with cellular tissue and the other without.

Marginal Vesicles and Membranes. The feature of the type species that immediately separates it from nearly all other stromatoporoids is the marginal membranes on the pillars and laminae. Other species of stromatoporoids have marginal cellules or cysts which may be analogous or ancestral structures. Lecompte (1952) and Galloway and St. Jean (1957) assigned species with marginal cellules and cysts to *Trupetostroma*. But as pointed out in the discussion of that genus, the vacuities in the tissue of the type species are not on the margins of the pillars. Lecompte believed that *Trupetostroma* gave rise to *Hermatostroma* by the enlargement of the vacuoles on the margins of the pillars and their coalescence into vesicles and membranes. In the absence of such structures in typical *Trupetostroma*, those species with cellules, vesicles, vacuoles, or membranes on the margins of the pillars are here considered to belong to *Hermatostroma* if they have spool-shaped superposed pillars and three-layered laminae. Transitional forms between *Trupetostroma* and *Hermatostroma* are probable, but the boundary between the two

genera should not be drawn where the laminae thicken to equivalence with the pillars, as recommended by Lecompte (1952), but between those species with marginal vacuities of any sort in the pillars and those without.

Conclusion. The genus *Hermatostroma* as presently constituted is polyphyletic and consists of a group of species with cellular tissue throughout (e.g. *H. beuthii*, *H. episcopale*, *H. parksi*, *H. porosum*, *H. maillieuxi*) and a group with marginal vesicles, vacuoles and membranes but compact tissue (e.g. *H. schlüteri*, *H. perseptatum*, *H. crassum*, *H. pustulosum*). The name *Hermatostroma* must be retained for the second group and a new name should be proposed for the first group with a type species chosen from among the new species in the list above.

AMPHIPORA Schultz

Type species: *A. ramosa* (Phillips)

Coenosteum columnar, rarely branching, with or without an axial canal, consisting of an amalgamate network of compact tissue which commonly is fibrous. Laminae cannot be distinguished and pillars diverging upwards and outwards from the axis are obscure and irregular. Some coenosteia have marginal cysts of the same tissue.

The type specimen of *Amphipora ramosa* has not been located. Although some specimens of Phillips's collection were found at Oxford, my inquiries did not uncover a specimen comparable to his illustration of this species. A specimen (No. 52873a) was found in the Geological Survey Museum, London, labelled '*Caenopora ramosa* Phillips, possibly syntype'. Although it cannot be positively identified with the type, since it has been cut on nearly all sides and polished, it is of similar size. The specimen supposed to be the other syntype is a tabulate coral. A well-preserved specimen from Devon, possibly from the Nicholson collection, must be established as a neotype for this widely distributed species when the genus receives revision. As nearly all specimens from Devon are recrystallized, the type specimen is unlikely to throw any light on the microstructure of the genus.

Most discussion of the genus has been centred around the extreme variability of its gross structure, reviewed by Lecompte (1952). Its microstructure is generally agreed to be fibrous with a dark line marking the axis of each structural element. In many of Nicholson's specimens from Germany, the central dark line is poorly defined and the microstructure is more like a water jet.

Yavorsky (1955) established the genus *Paramphipora* for stromatoporoids like *Amphipora* which do not have a dark axial line in the tissue. Other palaeontologists have been cautious about accepting this new genus, and the obscurity of the microstructure in many otherwise well-preserved specimens of the genus prompts me to withhold judgement until the Russian material has been examined.

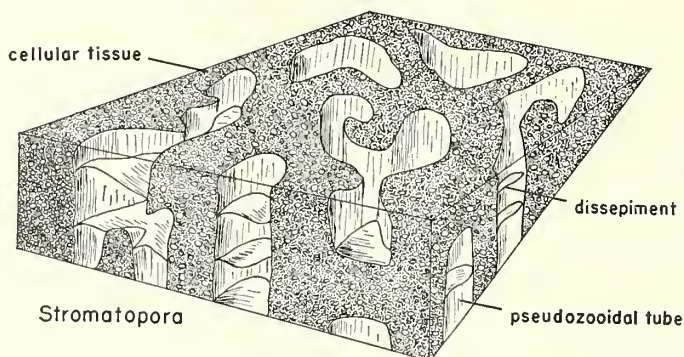
Lecompte (1952) believed that *Amphipora* is unique among the stromatoporoids both in microstructure and in gross structure. However, the gross similarity of *Amphipora* to many species of *Stachyodes* is striking and its microstructure closely resembles that of *Dendrostroma* and even that of *Anostylostroma* in certain states of preservation. These similarities leave little doubt that it is a stromatoporoid and suggest that it should be classified with these genera rather than in a separate family, or with the Idjostromatidae, to which it shows little relationship except in external form.

STROMATOPORA Goldfuss

Text-fig. 13

Type species: S. concentrica Goldfuss

Coenosteum composed of an amalgamate network of tissue in which neither laminae nor pillars are easily distinguished. Vertical elements (pillars) dominate the structure and are separated by high galleries called pseudozooidal tubes. Microlaminae, composed of a line of dark tissue, or more rarely a clear path in the tissue, are present in some species. Tangential sections show an irregular continuous network of tissue with small galleries and few areas of isolated tissue. The tissue is cellular or microreticulate.

TEXT-FIG. 13. $\times 50$.

Of the stromatoporoids, the genus *Stromatopora* has been by far the most difficult to restrict and the time for its dissection is overdue. Over two hundred species have been described and they are of such diverse form that no definition can cover them all.

The holotype of the type species, *S. concentrica*, is poorly preserved and has been differently described by Nicholson (1886, pp. 2, 3) and Lecompte (1952, p. 271). Nicholson interpreted the type, on the basis of topotypes (which he said were identical in all ways with it), as having a dominantly vertical structure with distinct pseudozooidal tubes. Lecompte stated that the type nowhere showed the dominantly vertical structures illustrated by Nicholson (pl. 11, fig. 18) and interpreted it on the basis of specimens from the Ardennes showing few or no pseudozooidal tubes. Galloway and St. Jean (1957) rejected Lecompte's interpretation and stated that his specimens from Belgium do not belong to *Stromatopora* at all but are *Ferestromatopora tyrganensis* Yavorsky. Because Nicholson's interpretation is based on topotype material and has been accepted as definitive for many years, it is here adopted.

The microstructure of the specimens (Nich. 1-5) from Gerolstein, Germany, on which Nicholson based his interpretation is flocculent with local suggestion of cellules. The tissue is not prominently speckled but, like much of the material from the Eifel, has an overall irresolvable brown stain. Little movement of this dark matter into the galleries has taken place. In the flocculent tissue clear areas appear commonly but the cellular nature is not preserved evenly throughout. The cellular microstructure is much better preserved

in those specimens from Gerolstein that Nieholson described as *S. concentrica* var. *colliculata* (a Devon specimen is illustrated in Pl. 17, fig. 6).

The cellular microstructure characteristic of *Stromatopora* and its change to melanospheric tissue is more fully discussed in the first part of this paper.

Microlaminae. Continuous laminar structures of three types are present in species of *Stromatopora*.

1. A thin line of granules making a more or less continuous dark plate (*S. divergens* Galloway and St. Jean, *S. dubia* Lecompte) (Pl. 17, fig. 7).
2. A clear zone running through flecked or melanospheric tissue (*S. mononensis* Galloway and St. Jean) (Pl. 14, fig. 5).
3. A series of darker and lighter zones caused by the regular arrangement of cellules and melanospheres (e.g. *S. concentrica colliculata* Nicholson, *S. eumaculosa* Galloway and St. Jean, *S. laminosa* Lecompte, *S. submixta* Galloway and St. Jean) (Pl. 18, fig. 3).

Galloway's (1957) definition of this genus emphasized the microlaminae and he believed that when they are not present [and they are not in such species as *S. hupschii* (Bargatzky), *S. bucheliensis* (Bargatzky), *S. concentrica* (Goldfuss) (sensu Nicholson)] they have been destroyed during preservation or resorbed during the life of the colony. Amalgamate tissue with marked lamination is characteristic of *Ferestromatopora* but the species which Galloway (1957) removed from *Stromatopora* to this genus (*S. marpleae* Galloway and St. Jean, *S. obscura* Galloway and St. Jean, *S. larocquei* Galloway and St. Jean, and *S. dubia* Lecompte) do not have the large galleries typical of *Ferestromatopora*. As the cellular nature of the tissue of these species is obscure, they are better considered to belong to *Clathrocoelona*.

Even if these species are eliminated from *Stromatopora*, species showing continuous microlaminae remain. Where microreticulation is well developed, as in such species as *S. laminosa* Lecompte, the dark matter between the horizontal rows of cellules may form a distinct microlamina. This microstructure is shown well by Silurian species of *Stromatopora*, such as *S. typica* Rosen. Microreticulate tissue might be the basis for the separation of a group of species from the main body of *Stromatopora* species. In some species with microreticulate tissue the microlaminae seem to be independent of this microstructure.

The characters which separate *Stromatopora* from the related genera *Syringostroma*, *Parallelopora*, *Taleastroma*, etc. are discussed under these genera.

FERESTROMATOPORA Yavorsky

Type species: F. krupennikovi Yavorsky

Coenosteum of amalgamate structure, horizontal structural elements predominating over vertical ones. Fibres of the tissue anastomose forming a fine continuous network enclosing irregular galleries that are not superposed to form pseudozooidal tubes. Microlaminae may be present. Microstructure is cellular.

Yavorsky (1955) compared the gross structure of *Ferestromatopora* with that of *Clathrodictyon confertum* Nicholson (better referred to *Stromatoporella* on the basis of the microstructure of the laminae) and in its thin, arched laminae and lenticular galleries this species is much like *F. krupennikovi*. In typical species of *Ferestromatopora* the

galleries are large, the tissue fibres are delicate, and form a fine three-dimensional mesh (e.g. *F. krupennikovi* Yavorsky, *F. tyrganensis* Yavorsky, *F. jacquesensis* Galloway, *F. contexta* Stearn). In tangential section the amalgamate structure forms a continuous network and no isolated pillars can be distinguished. The microstructure of typical species of *Ferestromatopora* is cellular, much like that of *Stromatopora*. It shows a marked tendency to become melanospheric during preservation.

Although typical specimens of *Ferestromatopora* are easily distinguished from typical ones of *Stromatopora* on the basis of the absence of pseudozooidal tubes and the dominance of horizontal elements, such species as *S. divergens* Galloway and St. Jean, *S. laminosa* Lecompte, and *S. eumaculosa* Galloway and St. Jean, whose microlaminae seem to be derived from microreticulate tissue, could be assigned to either genus. Such species can be assigned to *Stromatopora* if the galleries are superposed forming pseudozooidal tubes, and to *Ferestromatopora* if the tubes are missing. The splitting of this group with microreticulate tissue away from both genera seems to offer a solution to this problem that expresses the biological relationships more satisfactorily.

TALEASTROMA Galloway

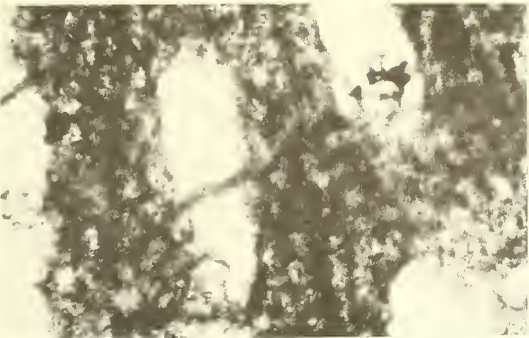
Type species: T. cummingsi (Galloway and St. Jean)

Coenosteum of amalgamate structure similar to that of *Stromatopora* with dominant vertical structural elements, pseudozooidal tubes, and dissepiments; traversed by short, slender, rod-like pillars circular in cross-section. Microstructure of amalgamate tissue and pillars is cellular.

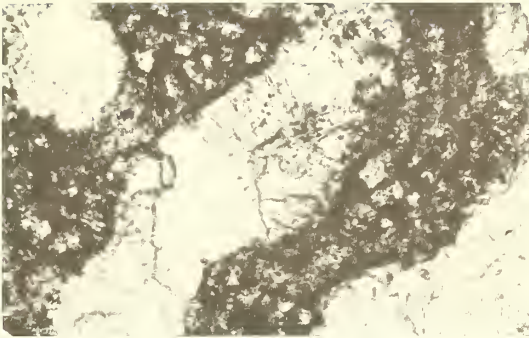
Galloway (1957) established this genus for the reception of three species that he and St. Jean (1957) had described as *Stromatopora* and two species described by Lecompte (1952) as *Stromatopora*. These species were separated from *Stromatopora* on the basis of their long pillars, which are compact axially and have borders of 'dark maculae'. In the type species, *T. cummingsi*, the melanospheres ('dark maculae') are well defined, locally closely set, locally widely separated and concentrated on the margins of the pillars (Pl. 18, fig. 5). In some places half a melanosphere at the edge of a pillar appears to be cut off by the boundary with the gallery. In tangential section the disposition of the melanospheres is not as obvious as in vertical section.

EXPLANATION OF PLATE 18

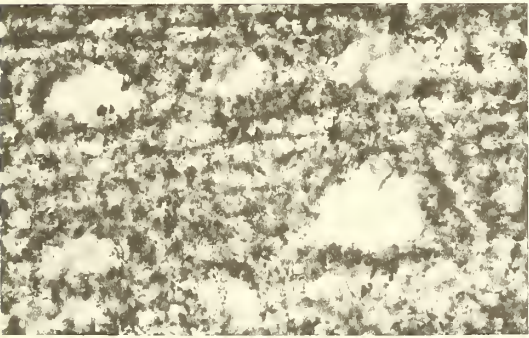
- Figs. 1, 2. *Stromatopora carteri* Nicholson (Nich. 37d, 37). Vertical and tangential sections, $\times 100$, showing cellular tissue of the pillars. Middle Silurian, Benthall, Shropshire.
- Fig. 3. *Stromatopora typica* Nicholson (Nich. 59b). Vertical section, $\times 100$, showing microreticulation. Middle Silurian, Oesel Island.
- Fig. 4. *Stromatopora typica* Nicholson (Nich. 49). Tangential section, $\times 100$, showing melanospheric microstructure. Middle Silurian, Ironbridge, Shropshire.
- Fig. 5. *Taleastroma cummingsi* Galloway and St. Jean (UNC 304-47). Vertical section of holotype, $\times 100$, showing pillars with peripheral melanospheres. Middle Devonian, 5 miles E. of Logansport, Indiana.
- Fig. 6. *Syriugostruma densum* Nicholson (Nich. 311g). Tangential section of holotype, $\times 50$, showing cellular microstructure. Middle Devonian, Kelly's Island, Ohio.
- Fig. 7. *Syriugostruma densum* Nicholson (UNC 306-8). Vertical section of topotype, $\times 100$, showing open cellular microstructure. Middle Devonian, Kelly's Island, Ohio.
- Fig. 8. *Stachyodes verticellata* (McCoy) (Nich. 394). Peripheral part of cross-section, $\times 50$, showing striated tissue. Devonian, Shaldon, Devon.



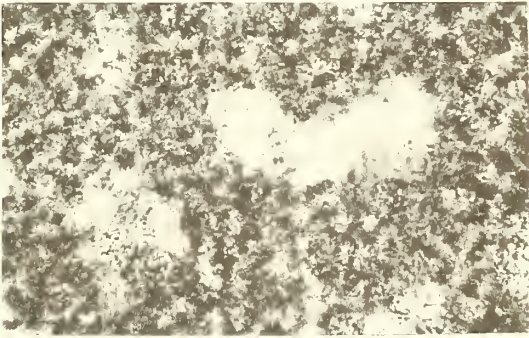
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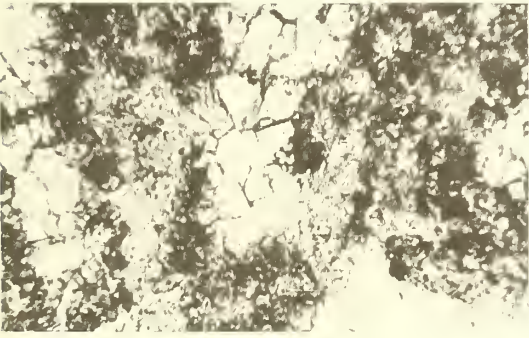
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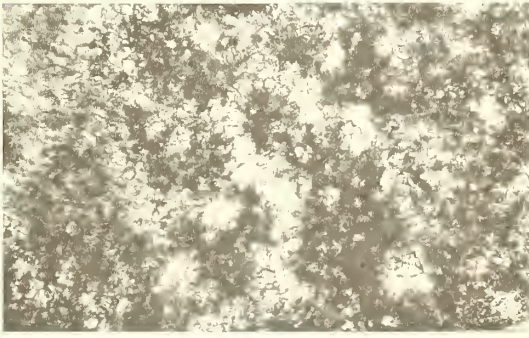
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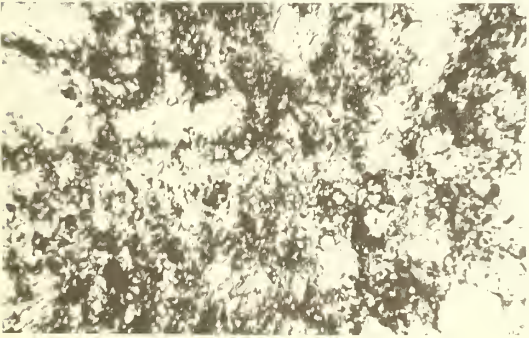
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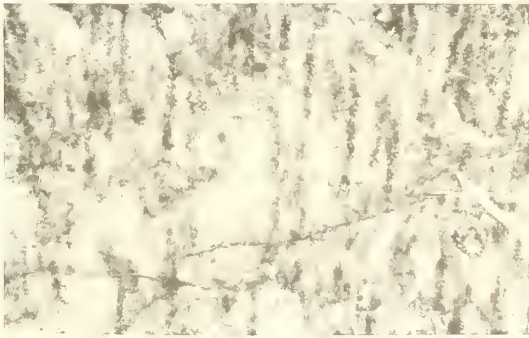
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8

In specimens of *Taleastroma pachytextum* (Lecompte) in the Galloway and St. Jean collection, generally the tissue is flocculent but the edges of the pillars contain melanospheres. The holotype of *T. pachytextum* was not examined but the Nicholson collection contains an interesting series of specimens of this genus identified by Nicholson as *Stromatopora beuthii* Bargatzky, some of which (Nich. 69, 74) were compared by Lecompte (1952) to *Stromatopora pachytexta*. Lecompte (1952) showed that Bargatzky's type of *S. beuthii* is a *Hermatostroma* but such specimens as Nich. 69, 71, 74, and 81, all from south Devon, show close affinities to *Taleastroma*. Some of these specimens are similar in microstructure to the American ones showing pillars with peripheral melanospheres and compact axes. Some pillars are marked with an axial dark line and water jet microstructure. Detailed description of these specimens and assignment of a name to them will have to await a complete revision of the stromatoporoid fauna of Devon.

The other two American species, *T. conicomamillatum* (Galloway and St. Jean) and *T. magnimamillatum* (Galloway and St. Jean), do not show the peripherally melanospheric microstructure as clearly as the first two.

In founding this genus Galloway emphasized the peculiar microstructure of the pillars, compact inside and 'maculate' outside. The genus, however, also differs from *Stromatopora* in the possession of rod-like pillars distinct from the amalgamate network. In this paper melanospheric tissue is regarded as a secondary microstructure produced during preservation and of doubtful generic significance. This view allows several interpretations of the microstructure of *Taleastroma*.

1. The pillars were originally completely cellular, the cellular tissue has changed to melanospheric, then the melanospheres were destroyed in the axes of the pillars.
2. The pillars were originally compact, and melanospheric alteration has affected only their peripheries.
3. The pillars were marginally vacuolate or cellular and this zone has become melanospheric.

If the third interpretation is accepted, *Taleastroma* would have to be placed in synonymy with *Hermatostroma*. The lack of marginal vacuoles or cellules in parts of *Taleastroma* specimens where marginal melanospheric microstructure is not developed does not support this interpretation. The combination of compact pillars with cellular amalgamate tissue demanded by the second interpretation is not found in other genera of stromatoporoids, for the two types of tissue seem to be mutually exclusive. Therefore, although it is not the simplest hypothesis, the first interpretation, that the peripherally melanospheric tissue has been derived secondarily from uniformly cellular pillars, is preferred.

As defined above the genus *Taleastroma* is a valuable one. It differs from *Syringostroma* in the lack of large, lacy pillars penetrating the structure, from *Parallelopora* in the lack of alignment of its smaller cellules, and from *Ferestromatopora* in its through-going pillars.

SYRINGOSTROMA Nicholson

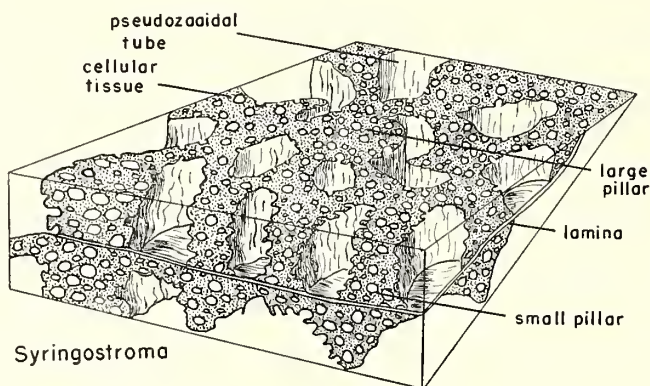
Text-fig. 14

Type species: S. densum Nicholson

Coenosteum an amalgamate structure, like that of *Stromatopora*, within which thick persistent pillars and laminae can be distinguished. Laminae composed of

thin dark or light microlaminae. Pillars thick, long, rod-like, traversing many laminae. Microstructure cellular or microreticulate.

Nicholson's choice of specimen (Nich. 311) as the type of *Syringostroma densum* was unfortunate as it is poorly preserved and its vague structure is open to different interpretations. The microstructure of the tissue is densely speckled and somewhat recrystallized. The tissue is faintly fibrous generally. One tangential section (Nich. 311g) shows coarsely cellular pillars (Pl. 18, fig. 6). In other sections the tissue seems at low power ($\times 10$) to contain melanospheres, but the melanospheric microstructure is not clear at



TEXT-FIG. 14. $\times 50$.

higher power. Thick, persistent pillars are crossed by fine, dark microlaminae (the structure is not well represented in Nicholson's illustration, 1886, pl. 11, fig. 14). Between the microlaminae the tissue is irregularly distributed, forming short vertical structures like pillars or coating the microlaminae to form thick laminae. Penetrating this whole structure are large, rod-like pillars with vague water jet microstructure. The microlaminae do not bend upwards into the pillars and may or may not cross them. In tangential section the pillars are circular darker areas in the irregular network of the amalgamate tissue.

Galloway and St. Jean (1957) have described a topotype (UNC 306-8 and 9 from Kelley's Island, Lake Erie), which is much better preserved than the holotype (Pl. 18, fig. 7). The amalgamate tissue is cellular and the speckled tissue between the cellules is reduced to lace-like form by the abundant cellules. The cellular tissue forms thick, short, spool-shaped pillars and locally is microreticulate. Some microlaminae are formed between two rows of cellules in this microreticulate tissue. The large pillars which traverse the coenosteum show neither cellular nor water jet microstructure.

Galloway (1957) believed that the distinguishing features of the genus *Syringostroma* are its microlaminae, which bend up into the pillars, and its long, thick columnar pillars. Several specimens at the University of North Carolina and at the British Museum (Natural History) show a vague water jet microstructure in the pillars that Galloway (1957, see pl. 31, fig. 15) apparently attributed to aligned melanospheres. As pointed out in the first part of this paper, the water jet microstructure is not confined to this genus but seems to develop under certain conditions in many genera that have columnar pillars.

In the examination of numerous sections of many species of this genus I found no evidence that the water jet microstructure was caused by the alignment of cellules or melanospheres. Ripper (1937*a*) and Lecompte (1952) noted the vague vertical structures in *Syringostroma* and Lecompte believed that this fibrous striation might indicate that the genus was related to *Parallelopora*.

Two other species described by Nicholson reflect his interpretation of the genus. *Syringostroma ristigouchense* (Spencer) from the Silurian of New Brunswick is only superficially similar to *S. densum*. It has large columnar pillars, but they are not associated with an amalgamate tissue between them nor with microlaminae. Laminae are formed by periodic processes extending from the pillars. The microstructure of the pillars is flocculent in the type specimens and the alignment of the specks suggests an outward spraying fibrosity. The gross structure of this species is much closer to that of *Parallelopora* than to that of *Syringostroma* and its assignment to that genus seems more appropriate. *Syringostroma nodulatum* (Nicholson) was originally described as *Stromatopora* (Nicholson 1891) but has been assigned by Galloway and St. Jean (1957) to *Parallelopora*. Cellular tissue is well preserved in Nicholson's specimens and a fibrous water jet structure also occurs. This species is closer to *Syringostroma* than to *Parallelopora* and does not show the coarsely cellular microstructure of the latter genus.

The views of Parks (1909) and Ripper (1937*a*, 1938) concerning the transition between *Syringostroma* and *Stromatopora* were reviewed by Lecompte (1952). Lecompte adopted a very different view of *Syringostroma* and believed that the essential features of the genus are the bifid (tripartite) nature of the laminae and the superposition of short pillars from one interlaminar space to another. He described the tissue as cellular ('alvéolaire') but does not believe the genus is closely related to *Stromatopora*. According to Lecompte it is more closely related to *Trupetostroma*, to which it gives rise in the Givetian. This interpretation of *Syringostroma* is not supported by the type species nor has it been used by any other palaeontologist. Because Lecompte's concept of the genus differs so greatly from theirs, Galloway and St. Jean (1957) have reassigned many of Lecompte's species to other genera, largely to *Stictostroma*. However, many of the species they reassigned are unlike *Stictostroma* in tangential section for they show a continuous network of tissue rather than pillars cut individually into circular or vermiform shapes. A revision of this group of species and similar laminate species now included in *Stromatopora* is badly needed.

In the species described by Galloway and St. Jean (1957) the specks in the tissue are so large that they obscure the other microstructures. A few have cellular tissue but many show only a vague fibrosity which seems to be formed by the alignment of the specks. In such species as *S. sanduskyense* Galloway and St. Jean the reticulate arrangement of melanospheres may form microlaminae. In *S. superdensum* Galloway and St. Jean the fibrosity seems to be most distinct where the melanospheric nature of the tissue is least well defined, but the fibrosity cannot be traced to the alignment of cellules or melanospheres. Some of the microlaminae in these species seem to be formed by the alignment of melanospheres from originally microreticulate tissue, others seem to be plates of dark specks independent of the microreticulation. In *S. fuscum* Galloway and St. Jean clear microlaminae present the same problems of interpretation as those in some *Stromatopora* species, such as *Stromatopora mononensis* Galloway and St. Jean.

Syringostroma can be distinguished from *Stromatopora* on the basis of the long

columnar pillars which penetrate the amalgamate network. It differs from *Parallelopore* in the smaller size of the cellulose in the tissue which do not reduce the pillars to a lattice. The pillars of *Talestroma* are smaller and shorter but otherwise the genus is very similar to *Syringostroma*. The microlaminae characteristic of *Syringostroma* are found in several other related genera but the two sizes of vertical elements, one in the amalgamate network and the other as through-going pillars, is unique to *Syringostroma*.

STYLODICTYON Nicholson and Murie

Type species: S. columnare (Nicholson and Murie)

Coenosteum composed of fine continuous microlaminae locally grouped into thicker laminae, regularly bent upward into and across prominent persistent mamelon columns. The columns are solid tissue without internal structure and form papillae on the upper surface of the coenosteum. The pillars are short, incomplete, and expand upwards. The fine laminae are locally coated with diffuse tissue which partly fills the galleries. The microstructure of the tissue is not well enough preserved for determination.

Nicholson (1886, pp. 79, 80) was uncertain of the position of this genus in the Stromatoporidae or the Actinostromatidae. This uncertainty and the subsequent hesitation of investigators to use the genus can be traced to the poor preservation of the type specimen (P6031, Nich. 340 in the British Museum (Natural History) labelled as the type in Nicholson's handwriting, with tangential and vertical sections). The laminae are of variable thickness and are composed of several microlaminae about $15\ \mu$ thick. These may join with more diffuse tissue to make laminar elements up to ten times this thickness. The pillars are composed of widely scattered specks. They are confined to an inter-laminar space and spread out against the lamina above. The mamelon columns are of speckled tissue of various densities showing water jet fibrosity. Some of the concentrations of specks might be called melanospheres. None of the tissue is obviously cellular or melanospheric.

In its short pillars combined with large through-going columns, in its laminae composed of microlaminae, and in its regularly upturned lamina, this species is a *Syringostroma*. Had the cellular nature of the tissue been preserved, no question of its generic nature would have arisen. It is similar to *Syringostroma tuberosum* Galloway and St. Jean but differs in the dimensions of internal structures and in external morphology of the coenosteum. Unfortunately it cannot be matched with any species described by Galloway and St. Jean (1957) from Ohio. *Stylodictyon* is a junior synonym of *Syringostroma* and is not a valid genus.

STACHYODES Bargatzky

Type species: S. ramosa Bargatzky

Nicholson (1886) placed *S. ramosa* Bargatzky in synonymy with *Stromatopora* (*Caenopora*) *verticellata* McCoy. Since then the type species has been considered to be *S. verticellata*, but E. H. Flügel is investigating the problem of whether these two species are identical.

Coenosteum dendroid, fasciculate, or rarely massive. Each column typically has an axial canal or canals from which lesser canals branch towards the periphery.

Tissue is thick, filling most of the coenosteum apart from the canals, striated, that is traversed by dark, fine rod-like concentrations of specks or tubes which spray outwards and upwards from the axis of the column. Galleries small or absent. Laminae thin lines of dark granules, asymptotic to the periphery, restricted to the peripheral area, poorly developed, forming invaginating paraboloids about the axis of the columns. Thick pillars recognizable only near the periphery, oriented at right angles to the laminae, forming a continuous network in tangential sections.

Nicholson (1886) considered the striated tissue of *Stachyodes* to be diagnostic of the genus but other writers have emphasized the indistinctness of the pillars and laminae of *Stachyodes* as separating it from other dendroid stromatoporoids. Bargatzky's type of *S. ramosa* in the Bonn University collections is accompanied by two slides which are small but show the striations in the tissue spraying outward from the axis of the column. Laminae are absent in these two inadequate sections but growth stages are indicated by variations in the density of the tissue.

Nicholson believed that the striations in the tissue are tubules that have been filled with opaque matter, but in his specimens labelled *S. verticellata* (McCoy) from Shaldon (Devon) they are rod-like concentrations (15 μ in diameter) of dark specks (1 μ across) (Pl. 18, fig. 8). In tangential section they are round dots of dark tissue on a light background. Locally the dots are arranged in a circle or form a rough network. Nicholson's collection also contains a specimen (Nich. 397) from Hebborn (West Germany) in which the tissue is not speckled but a dark brown colour. In this specimen striated microstructure seems to be caused by light-coloured rods or tubules 30–50 μ across rather than by dark rods in a lighter tissue. Tissue reversal is thus found in *Stachyodes* as in many other genera. The better preservation of the German specimens suggests that the tubules represent the original state of the tissue and that the rods may be analogous to melanospheres. Lecompte (1952) believed that the fundamental microstructure of *Stachyodes*, like that of many other stromatoporoids, is microreticulate rather than striated. He described specimens showing transverse lines which cut the longitudinal striations, producing a microstructure that he compared with that of *Parallelopora*. The description by Galloway and Ehlers (1960, p. 102) of the microstructure of *S. paralleloporoides* Lecompte as composed of 'superposed maculae much as in the genus *Parallelopora*' may also refer to this texture. The microreticulate nature of the tissue and its relationship to *Parallelopora* is not confirmed by either Bargatzky's or Nicholson's material.

Lecompte does not agree that striated tissue is characteristic of *Stachyodes* alone because two species that he places in *Idiostroma* also show it. The relegation by Galloway and Ehlers (1960) of the two species in question (*I. crassum* Lecompte, *I. irregularis* (Heinrich)) to *Stachyodes* helps to maintain the homogeneity of both genera with respect to microstructure, but the appearance of striated tissue in the holotype of *Idiostroma caespitosum* shows that the distinctness of microstructure of the two genera may be difficult to maintain.

Galloway and Ehlers (1960) described the tissue of *Stachyodes* as porous with pores parallel to the axis in the axial regions and perpendicular to it in the peripheral region. The pores referred to are presumably the tubules described by Nicholson.

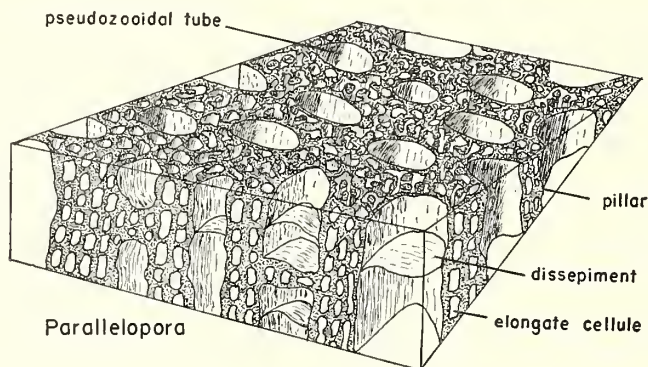
Most species of *Stachyodes* are columnar or dendroid but in some, such as *S. fasciculata* Heinrich, the tissue is continuous between the columns, which are merely high mamelons in a massive coenosteum. Such specimens illustrate the difficulty of basing generic distinctions on the form of the coenosteum. The axial tube is not present in all cross-sections of the columns of *Stachyodes* and its presence or absence is not a valid generic character in this or other genera.

PARALLELOPORA Bargatzky

Text-fig. 15

Type species: P. ostiolata Bargatzky

Coenosteum of amalgamate structure with thick, continuous, long pillars and thick laminae generally composed of microlaminae. Tissue microreticulate and cellules large, comparable in diameter to thickness of pillars. Cellules of pillars so large and closely spaced that they reduce darker speckled tissue to a tenuous three-dimensional lattice of strands and rods or to subspherical melanospheres.



TEXT-FIG. 15. $\times 50$.

The distinctive features of the genera *Parallelopora*, *Stromatopora*, and *Syringostroma* have been a matter of discussion ever since late in the nineteenth century. Recent discussions of the problem can be found in Yavorsky 1963, Lecompte 1951–2, and Galloway 1957. Lecompte reviewed the older literature and concluded that the separation of *Parallelopora* from *Stromatopora* was of doubtful validity and the only feature which might justify *Parallelopora* would be the dominance of vertical pillars in its structure. His viewpoint depended on his interpretation of the type of *Stromatopora concentrica* Goldfuss as not showing such vertical structures (see above). Yavorsky believed that *Parallelopora* shows many differences from *Stromatopora* in the net-like structure of the coenosteum, the predominance of the pillars, their coarser porosity, and the ampullae. Galloway emphasized as typical of *Parallelopora* its pillars ‘composed of small, parallel, vertical tubules and vertical rods or columns of dark dots’ (1957, p. 450). Some species, such as *Parallelopora nodulata* (Nicholson), have been at one time or another assigned to all these genera. Yavorsky (1963, p. 18) stated that the type species, *P. ostiolata*, is not typical of the genus!

The differences of opinion concerning *Parallelopora* have stemmed from the assignment to this genus by palaeontologists starting with Nicholson of species which resemble the type species only slightly. The type specimen and sections of *P. ostiolata* are in the Bonn University collections but sections of the type are also in the Nicholson collection at the British Museum (Natural History). Pillars are the most conspicuous element of the structure and horizontal elements are restricted to dissepiments and latilaminae. In most places the dark material of the pillars seems to be arranged as bundles of rods and large melanospheres, but where preservation is better, both in Nicholson's and Bargatzky's slides, the pillars can be seen to contain two or three vertical rows of large cellules (Pl. 19, figs. 8, 9). These are so large that they reduce the dark material between them to a series of rods and subspherical areas of speckled tissue. The cellules are commonly elongated vertically and may join in vertical series to make tubules. The pillars are so reduced by the cellules that their outlines are obscure and the cellules can be confused with the superposed galleries that form pseudozooidal tubes. In tangential section the pillars join into a continuous network. In this tissue are large melanospheres (30 μ across) composed of fine specks (less than 1–3 μ across). These melanospheres are largely discrete in Nicholson's slide (Nich. 125) but in Bargatzky's slide the transition from tissue in which the melanospheres are not joined, to tissue in which the darker areas enclose cellules, can be seen locally. The microstructure of *Parallelopora* is established by the type species as being essentially microreticulate like other related genera, but is distinctive in the size of the cellules which reduce the pillars to a three-dimensional lattice.

Bargatzky described three other species of *Parallelopora*. *P. stellaris* is represented in his collections by a specimen and tangential section but no vertical section appears to have been cut. The broken surface of the specimen, however, shows coarsely cellular pillars with ragged borders and poorly developed laminae. The tangential section is much like that of *P. ostiolata* but shows well-developed astrorhizae. Slides of the type of *P. goldfussi* Bargatzky both in Bonn and London show that it is similar in microstructure to *P. ostiolata* (Pl. 19, fig. 3). It has thick pillars containing large cellules arranged in vertical series which tend to join into tubules. Lecompte (1952) pointed out that the last species described by Bargatzky, *P. eifeliensis*, is probably the same as *Stromatoporella eifeliensis* Nicholson. Lecompte referred *Stromatopora bucheliensis* Bargatzky to *Parallelopora* but its cellular microstructure is much finer than that which would qualify it for inclusion in the genus as here defined.

Nicholson referred several specimens with poorly preserved microstructure from Devon to *Parallelopora*. Those referred to *P. dartingtonensis* (Carter) have already been discussed under *Trupetostroma*. Those referred to *P. capitata* (Goldfuss) are a diverse group, none of which belongs in this genus. Nicholson's specimens of *P. capitata* from Germany have been assigned by Lecompte to a new species, *Trupetostroma thomasi* Lecompte.

The species of *Parallelopora* described by Galloway and St. Jean (1957) from the mid-western United States are closely related to the type species. *P. campbelli* Galloway and St. Jean and *P. typicalis* Galloway and St. Jean show a vertical alignment of large cellules. In *P. pulchra* Galloway and St. Jean microreticulate tissue is well developed and continuous microlaminae are prominent. *P. nodulata* (Nicholson) and *P. eumamillata* Galloway and St. Jean do not have the generic characters of *Parallelopora* (the large

cellules and microreticulate tissue) as well developed, and show some resemblance to *Syringostroma*.

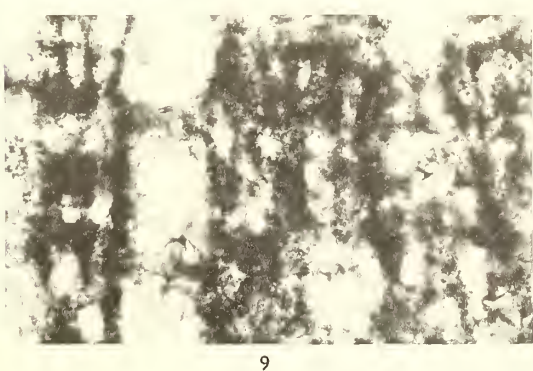
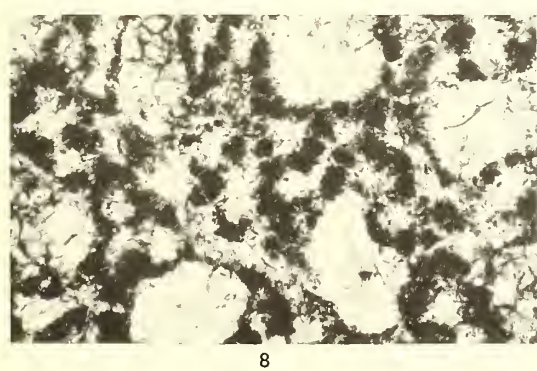
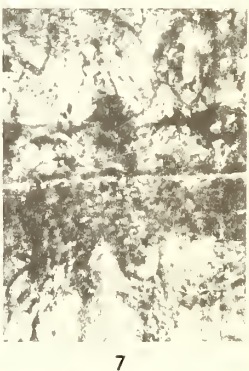
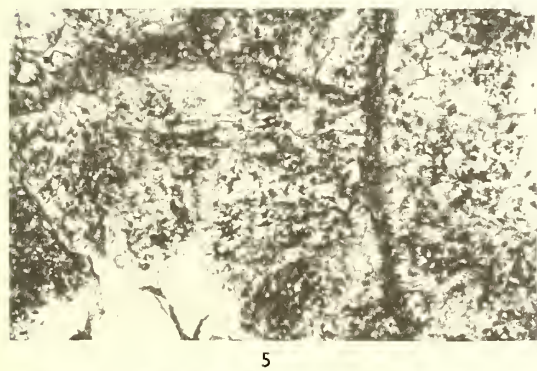
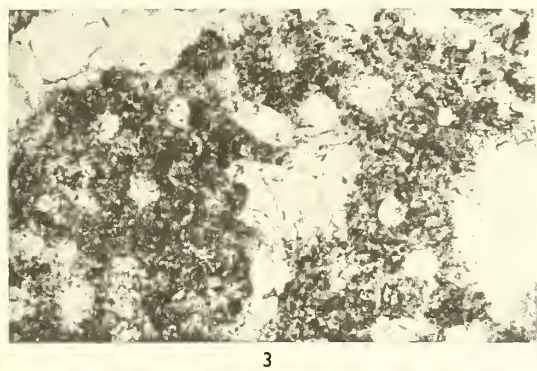
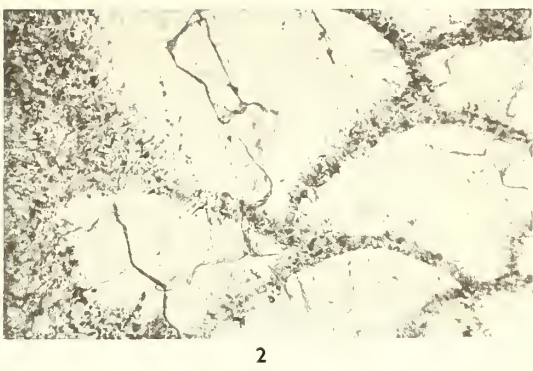
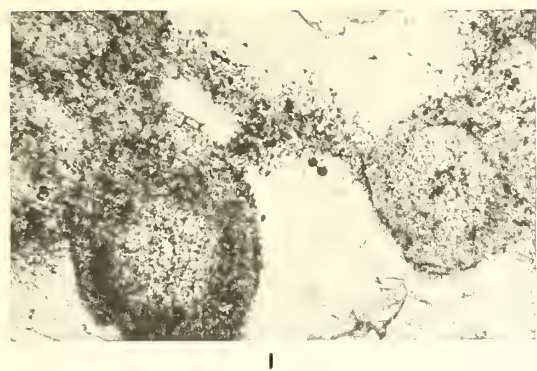
Family LABECHIIDAE Nicholson

The genera of this family are considered together since their structures and microstructures are similar. Their coenostea are composed primarily of overlapping cysts, which may be of small radius as in *Cystostroma* Galloway and St. Jean, or long and low as in *Rosenella* Nicholson and *Pseudostylodictyon* Ozaki. The cysts may form laminar coenostea as in these two genera or they may build a cylindrical coenosteum around a line of larger cysts as in *Aulacera* Plummer (formerly *Beatricea* Billings) and *Cryptophragmus* Raymond. They may be penetrated by through-going pillars of lamellar form as in *Stromatocerium* Hall. They may have minute denticles or villi on their surfaces (*Rosenella* and *Cystostroma*). The microstructures of the cysts and the pillars are the subject of the following discussion.

The type species of *Labechia* Edwards and Haime, and therefore the standard for comparison in the family, is *L. conferta* (Lonsdale) from the Wenlock limestone (Middle Silurian) of Shropshire. Lonsdale's specimens were not located. In topotypes of *L. conferta* from the Nicholson collection the pillars are a light brown colour and are full of small specks, from 5 to less than 1 μ across, which have diffused slightly into the galleries. The pillars have zigzag edges and extend in a sort of buttress where each cyst joins (Pl. 19, figs. 1, 2). The cysts have sharp boundaries, are about 30–45 μ thick and are composed of a single layer of speckled compact tissue. The labechiid stromatoporoids are generally poorly preserved but the preservation of these specimens is exceptionally good. In many of them the crystal boundaries of the infilling calcite are completely independent of the structure of the stromatoporoid. In tangential section the pillars show a slightly differently coloured central area or several vaguely defined concentric zones of different density. The concentric zones are poorly defined in vertical section where they appear as upward pointing, invaginating cones. They mark lines of growth of the pillars and do not demonstrate that the pillars were hollow. In most states of preservation the

EXPLANATION OF PLATE 19

- Figs. 1, 2. *Labechia conferta* (Lonsdale) (Nich. 264, 264b). Tangential and vertical sections, $\times 50$, showing compact tissue, concentric zones of the pillars, and single layered cysts. Middle Silurian, Dudley, Worcestershire.
- Fig. 3. *Parallelopore goldfussi* Bargatzky (Nich. 106). Tangential section, $\times 100$, showing large cellules up to 50 μ across. Middle Devonian, Steinbreche, Germany.
- Fig. 4. *Aulacera cylindrica* (Foerste) (UNC 302–74). Vertical section of a large cyst, $\times 100$, showing the migration of specks out into the gallery and the independence of crystal boundaries. Upper Ordovician, 2 miles SW. of Deatsville, Kentucky.
- Fig. 5. *Aulacera nodulifera* (Foerste) (Nich. 289, *Beatricea undulata* of Nicholson 1886). Cross-section of cysts, $\times 100$, showing bursts of diffusing specks. Upper Ordovician, Kentucky.
- Figs. 6, 7. *Rosenella macrocystis* Nicholson (Nich. 280). Two vertical sections in the same slide, the first showing no diffusion of specks due to the filling of the galleries, and the second showing diffusion into the galleries where they are filled with calcite. Middle Silurian, Gotland.
- Figs. 8, 9. *Parallelopore ostiolata* Bargatzky (Nich. 125, 125a). Tangential and vertical sections of holotype, $\times 100$, showing large vertically aligned cellules. Middle Devonian, Büchel, Germany.



cysts look dark against the light background of the galleries but in some specimens the cyst may appear lighter than its halo of diffusing specks.

In some species and specimens of *Labechia*, e.g. *L. macrostyla* Parks, *L. huronensis* (Billings) (Nich. 277a), and in *Labechiella serotina* (Nicholson), the cysts have the appearance of those in *Labechia conferta*; in most other species and in other genera of this family their appearance has been altered. Commonly the cyst appears in vertical section as a thin dark line of specks bordered on either side by thicker layers of speckled tissue. The outer edge of these layers is abrupt but is not marked by a darker membrane or suggestion of a tissue boundary (Pl. 19, fig. 4). The speckled layer on the concave side of a cyst is usually thicker than that on the convex side and not uncommonly is so thick that it almost fills the gallery. The density of specks in these two belts is uneven and transverse clear areas may cross them. The specks may be arranged in fibrous groups ('bursts') which converge on the cyst surface (Pl. 19, fig. 5). In tangential section the groups are circular concentrations of specks whose fibrosity is unrelated to adjacent concentrations.

The speckled layers have been interpreted by Galloway and St. Jean (1961) and Nicholson (1886) as part of the original structure of the coenosteum. That these cysts were originally single layers of tissue and that the layers are zones of diffusion of specks from the cysts and therefore a result of the process of preservation is shown by the following evidence:

1. The speckled layers are not shown by the type species of *Labechia* and several other species and specimens which are much better preserved than the specimens which show the layers.

2. The diffuse layers of speckled tissue around the laminae and cysts are common to nearly all genera of Palaeozoic stromatoporoids and have no morphologic significance.

3. In many specimens the 'bursts' of specks are related to the pattern of crystals in the calcite which has infiltrated the fossil. Specimens of this family in which the crystal mosaic is independent of coenosteal structure are rare; in most specimens a line of small crystals has first developed along the edges of the galleries and later the rest of the galleries have been filled with large clear crystals. The diffusion of specks seems to have taken place during the first phase of gallery filling. In the very rare cysts where the boundary of the speckled layers is marked by a dark line, the line seems to be the boundary of a single crystal or a set of crystals. More commonly the specks end just within the boundary of the crystals lining the galleries. Each diverging group or 'burst' of specks is limited to a single such crystal. Why the specks are arranged in a diverging pattern and do not reach the edge of the crystal is yet to be explained but their arrangement is easy to observe.

4. Transverse clear zones along the layers which were interpreted by Galloway and St. Jean (1961) as pores, are related to crystal boundaries and are due to the division of the layer into diverging groups of specks.

5. Where sediment fills the galleries of specimens, and it commonly does in this family, the layers are missing and no migration of specks has taken place (Pl. 19, figs. 6, 7).

Although the diffusion layer on the concave side is generally thicker, comparable 'bursts' of specks may also extend from the convex side of cysts. Perhaps the focusing of diffusion forces from the concave surface has concentrated them and moved the specks further than on the convex side. Gravity is not likely to be an agent causing this asymmetry, for the concave side is not the downward side in all labechiids, but in columnar coenostea, like *Aulacera*, the concave side is inward and the convex side outward.

Nearly all cysts in the Labechiidae (except in the genus *Forolinia* Nestor) appear to be without pores but one or two specimens in the Galloway and St. Jean collection show a well-defined perforation in the central dark line of a cyst. Such a rare structure could

be pathologic. How the living surface of the animal maintained contact with the tissue within the coenosteum in the general absence of such pores is a mystery. Perhaps the living tissue occupied only the surface. In this family, more than in any other group of stromatoporoids, sediment has infiltrated the coenosteum. Nicholson (1886) illustrated specimens in which all the galleries have been filled with micrite and specimens showing zones and even isolated chambers so filled are common. In *Aulacera* and *Cystostroma* layers of sediment occur in nearly all coenostea. How sediment which is rare in other stromatoporoid coenostea has infiltrated a structure which is less porous than all others is an unsolved problem.

The pillars of this group are rarely well preserved and in some genera are nearly always dissolved away during preservation. Nicholson (1886) found some in *Aulacera* but most specimens do not show them. In several species of *Stromatocerium* (e.g. *S. canadensis* Nicholson and Murie) they have been replaced or dissolved and are now areas of crystalline calcite.

Nestor (1964) interpreted the pillars of *Stromatocerium* as hollow and developed by superposed upturnings of the laminae or cysts. This may be true of some species but species like *Stromatocerium platypilae* Galloway have solid pillars and those of *S. leiper-sense* Galloway and Ehlers seem to be penetrated by tubules. Those of other species may contain dark streaks that suggest remnants of original tissue. The crystalline texture of the pillars in most specimens may be explained by the poor calcification or aragonitic nature of the original material.

The preservation of *Cystostroma*, *Aulacera*, and *Cryptophragmus*, where organized tissue occurs only here and there in a crystalline or sedimentary groundmass, shows that the earlier members of this whole family were poorly calcified.

Other pillar-like structures are found in the genus *Rosenella* Nicholson and in *Cystostroma simplex* Galloway and St. Jean. In the former denticles arising from the cysts are composed of speckled tissue like that of the cysts. In most specimens the upper boundary of the cyst to which the denticles are attached shows more diffusion of specks than the sharp boundary on the lower side of the cyst. The 'villi' of *Cystostroma simplex* which extend upwards from the cysts as little fingers into the gallery above, consist of microcrystalline aggregates embedded in the coarsely crystalline gallery filling. Another curious vertical structure was described by Nicholson (1886a) in *Rosenella platyphylla* Nicholson. This species has been made the type of the new genus *Forolinia* by Nestor (1964). In the holotype (Nich. 283) the low cysts are locally thickened by tissue with vague vertical markings, but no solid pillars exist. If the structure that Nestor interprets as superposed foramina in the cysts represent leached or recrystallized pillars, then the genus would be difficult to distinguish from *Labechia*.

An anomalous structure was described by Nicholson (1886) on a single specimen of *Aulacera undulata* (Billings) from Anticosti. He regarded it as a peripheral phase of *Aulacera* but as it is not found on other specimens of the species it is here considered to be an associated organism of unknown affinities.

CONCLUSION

Before any classification of the stromatoporoids can be based on microstructures a clear distinction must be made between those microstructures that were secreted by the

organism and those imposed on the tissue during the process of preservation of the hard parts. During this study some microstructures have been determined as original, some as formed during preservation, and some as both original and preservational. The following kinds of tissue are primary in the sense that they are believed to have been secreted by the organism:

compact, cellular and microreticulate, vacuolate, ordinicellular, striated, tubulate, peripherally vesicular.

The following kinds of tissue are secondary in the sense that they have been produced in whole or in part by the processes of preservation:

water jet fibrous, flocculent, pseudotubular, melanospheric.

The following kinds of tissue are both primary and secondary:

fibrous, tripartite laminae, transversely porous.

Fibrosity in such genera as *Anphipora*, *Hammatostroma*, and perhaps *Anostylostroma*, seems to be primary but the fibrosity developed in *Syringostroma*, *Stromatoporella*, and other genera has formed during preservation. Water jet microstructure is apparently always secondary in Palaeozoic stromatoporoids. Transversely porous tissue definitely forms secondarily from ordinicellular laminae but may also be a primary microstructure in such genera as *Gerronostroma*. Laminae with an axial dark or light line may be formed by the coalescence of a single line of cellules or may possibly also represent a primary microstructure.

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AN IMPROVED METHOD OF ANALYSING DISTORTION IN FOSSILS

by KLAUS SDZUY

ABSTRACT. Fossils distorted by tectonic strain can be reconstructed to their original shape if the strength and direction of the principal axes of strain are known. The ratio and orientation of the principal strains can be calculated by measuring the distortion in the angle between the median and transverse line in bilaterally symmetrical fossils like brachiopods and trilobites by several methods:

- a. They can be determined with exactitude if two such fossils are found on one bedding plane.
- b. If a number of single fossil specimens is available, but the relative orientations of their median and transverse lines from specimen to specimen are unknown, the amount of deformation can be calculated by Breddin's method, making use of the most strongly deformed former right angle in the collection.
- c. When the principal strain ratios have been calculated, the orientations of the principal axes of strain can be determined in any single specimen.

The different processes are greatly simplified by a special device described in the text.

IN 1962 I described a method for determining the amounts and orientations of the principal strains produced by homogeneous strain in bilaterally symmetrical fossils if two such fossils are found on the same bedding plane. A method based on the same principle was first employed by Lake (1943) who applied it to cases where one of the two fossils had remained right angled. When I wrote my first paper on the subject I was unaware of Lake's work.

The methods described in 1962 give good results, but they are time-consuming. For palaeontologists who have frequently to deal with distorted fossils, as well as for structural geologists who may wish to use distorted fossils to determine the amount of compression of rocks, speedier methods are desirable. Rapid methods for calculating the strains are presented in this paper. When the amount of distortion has been calculated the original form of the fossil may be reconstructed using the techniques employed by Lake (1943), and Sdzuy (1962), and other authors cited by the latter.

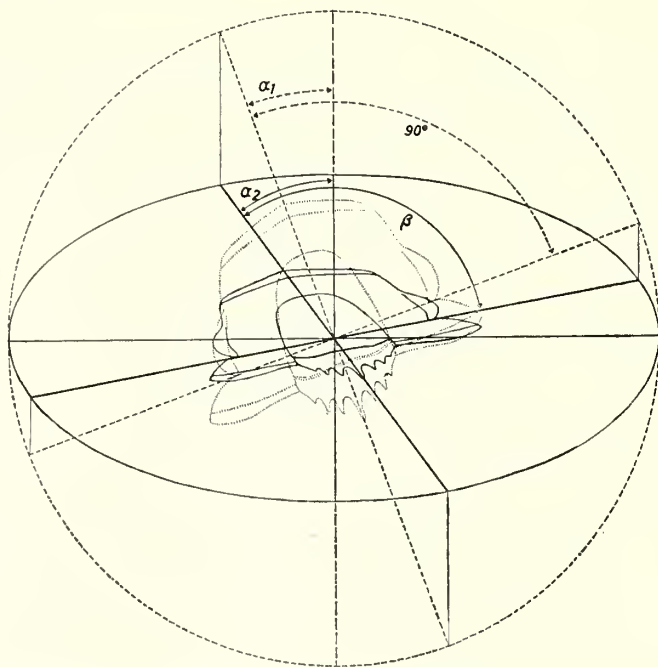
Distortion of fossils is rather the rule in geosynclinal strata. In Cambrian strata from different regions of Spain, for instance, deformation of about 60–70% is frequent.

THE PRINCIPLE EMPLOYED

For determining the amount of distortion only the angle between median and transversal direction in bilaterally symmetrical fossils need be measured. This angle may be called β ; it is constantly 90° in undistorted specimens. In deformed fossils β may remain 90° , or it may be either increased or decreased, and it can be measured directly in the distorted specimens (text-fig. 1). There are for each fossil two complementary angles β , enclosing together 180° . The tables, etc., in this paper are calculated for the obtuse angle β .

D indicates the amount of deformation as expressed by the ratio of the shortest to the longest axis of the strain ellipse. $D = 50\%$ could mean that the specimen has been compressed to 50% of its original extent parallel to the short axis of the ellipse and remained

unchanged parallel to the long axis. The direction of the short axis may then be presumed to be identical with the direction of deformation. A ratio of 50% could also have been produced if the specimen is stretched to 200% of its original extent parallel to the long axis and left unchanged parallel to the short axis of the ellipse, and still other processes are possible. The fossils restored by the methods described here will in any case show the original ratio of length/width.



TEXT-FIG. 1. Relationship between undistorted and distorted fossil.

Interrupted lines: Undeformed cranium of a trilobite drawn into a circle. Its main axes (transverse and median) include a right angle; the main axes include with the direction of later principal strain two acute angles α_1 (only one of these complementary angles is indicated).

Full lines: Effects of deformation ($D = 50\%$). The circle is deformed into an ellipse. The right angles between the main axes of the fossil are changed into angle β (only obtuse angle β indicated). Angle α_1 is changed into angle α_2 .

The size of β depends not only on the amount of deformation (D), but also on the size of the angle between the sides of β and the direction of principal elongation (text-fig. 1). If this angle is 0° , that is if one of the sides of the original right angle is parallel to the direction of deformation, β will be a right angle regardless of the amount of deformation. The angle β is made up of two angles, α_1 and $90 - \alpha_1$ before deformation, and α_2 and $\beta - \alpha_2$ after deformation. The effects of deformation (D) upon angle α_1 can be expressed as follows:

$$\tan \alpha_2 = \frac{\tan \alpha_1 \cdot 100}{D} \quad \text{and} \quad \tan(90 - \alpha_2) = \frac{\tan(90 - \alpha_1) \cdot 100}{D}$$

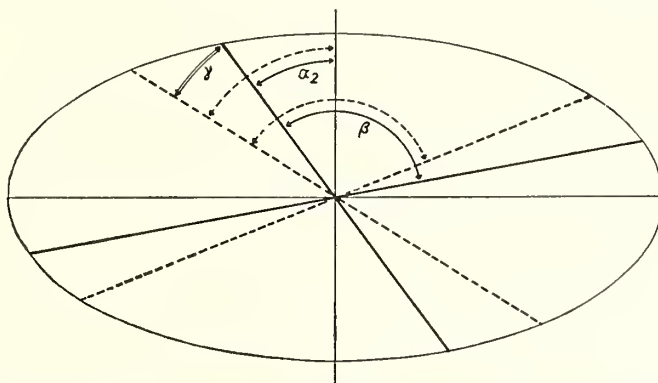
$$\left[\text{or } \tan(90 - \alpha_2) = \frac{\cot \alpha_1 \cdot 100}{D} \right].$$

At a given amount of deformation β is greatest if α_1 was 45° . Since $\tan 45^\circ$ (and $\cot 45^\circ$) equals 1,

$$\tan \alpha_2 (\text{or } \tan \frac{1}{2}\beta) = \frac{100}{D}.$$

Text-fig. 3 shows the combinations β/α_2 at deformations ranging from $D = 100\%$ to $D = 35\%$. A similar figure was published by Breddin (1956, fig. 32).

Since the deformed angle β depends on both D and the size of angle α , different combinations of these two factors may produce the same angle β . Consequently, the amount and direction of the principal strains cannot be deduced from a single angle β .



TEXT-FIG. 2. An ellipse obtained by deformation of a circle, with two different angles β (former right angles deformed by the same strain) drawn (one indicated by a dashed line, the other by a full line). The two angles β are at different angles (α_2) to the direction of principal strain, and consequently their size also differs. The two different angles β and angle γ can be measured in specimens; angle α_2 (necessary for reconstruction of the fossils) can then be calculated.

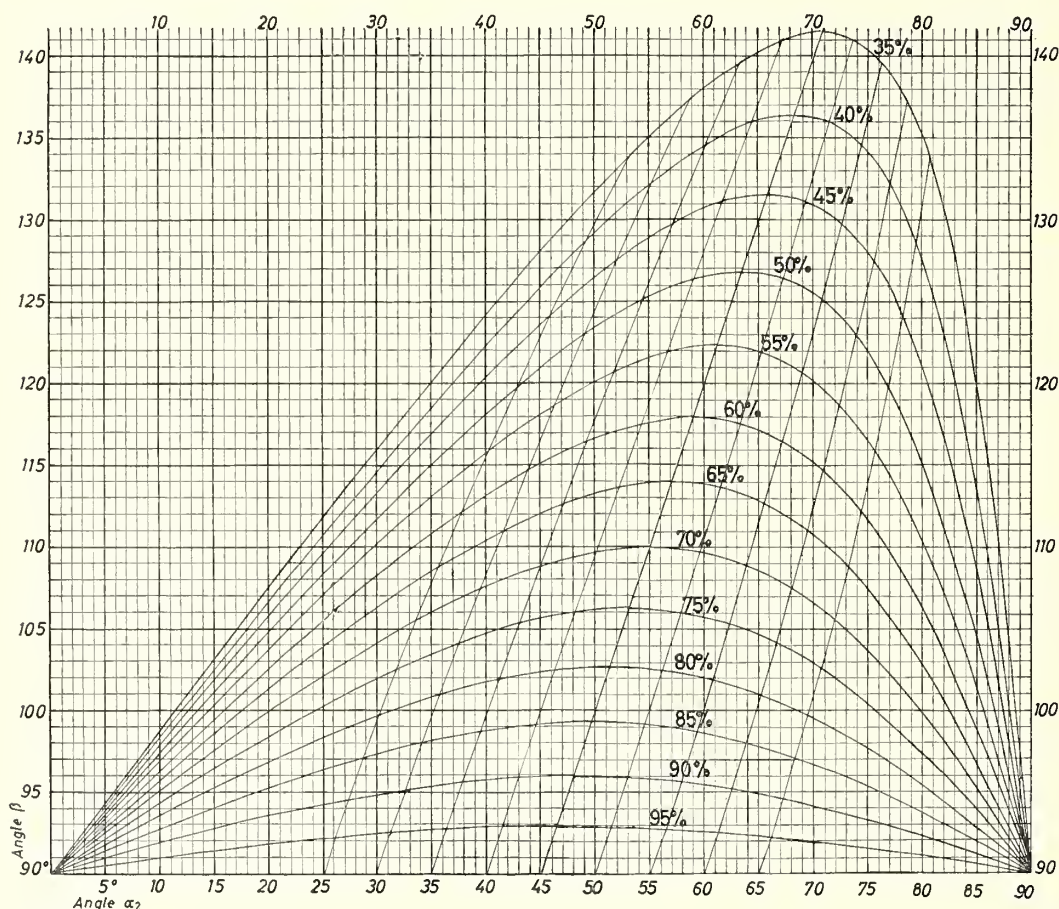
Two fossils on the same bedding plane which have two different angles β are, however, sufficient to determine with exactitude D and α . The relations between two such different angles β , produced by the same process of deformation, may be expressed by angle γ (text-fig. 2), which is equivalent to the difference between the two corresponding angles α_2 and which may be measured in the specimen.

If two different angles β and angle γ are known, D and α can be calculated. The mathematical process is, however, tedious to manipulate and will not be treated here because the indirect methods to find D and α described below and in my 1962 paper are easier and much faster to use. Slight inexactitudes inherent in these methods do not matter because they do not exceed the errors in measuring the different angles in the deformed specimens.

METHODS TO DETERMINE D AND α

1. *If angle γ is not known.* A single angle β does not allow determination of D or α . If, however, a sufficiently large number of specimens showing a single angle β each are at hand and if the mode of their occurrence (same bed and outcrop, homogeneous rock, etc.) indicates that they have been subjected to the same deformation, a method described by Breddin (1956, pp. 264–6) will allow the determination of D and α . It is only necessary to measure the most strongly deformed angle β in the material. If the material consists

of a large number of specimens, one may suppose that in the fossils with the most strongly deformed angle β , angle α_1 was close to 45° , and angle α_2 equals $\frac{1}{2}\beta$. D may then be estimated using text-fig. 3 (the apex of the curves representing D in the graph indicates the most strongly deformed angle β on the vertical scale of the graph), or it may be



TEXT-FIG. 3. Graph showing the possible combination of angles β and α_2 at deformations ranging from $D = 35\%$ to $D = 100\%$. The graph has been calculated for the obtuse angle β and for the two angles α_2 that make up the obtuse angle β . The lines ascending from the bottom line towards the upper right represent the progressing deformation of angle α_1 into α_2 .

calculated: $D = (100/\tan \frac{1}{2}\beta)$. The same equation, but with different symbols and another expression of D , was given by Breddin (p. 266). The device described below offers a quick way of measuring β , of discovering the most deformed angle β and computing the value of D .

When D has been calculated, angle α_2 can be found for any specimen showing a deformed angle β by using the device described below. The graph, text-fig. 3, can also be used for that purpose. The intersection between the curve representing D and the horizontal line representing angle β as measured in the specimen will indicate angle α_2 .

on the horizontal scale. Therefore, if D has been determined for a single specimen (or pair of specimens), all other specimens incorporating a former right angle and subjected to the same deformation can theoretically be restored. In practice, however, a serious drawback to this method is the fact that it is not known from which side of angle β that angle α_2 has to be measured. If angle α_2 is measured from the wrong side of β , β will be a right angle in the restored specimen, but the deformation concerning the ratio length/width of the specimen will be increased instead of eliminated. This effect is nil if the angle α_1 was originally 45° and it increases with decrease in the value of α_1 . Where angle α_1 was small (and consequently angle β does not differ much from a right angle), experience with the fossil in question will usually show which position of angle α_2 is the right one.

2. *If angle γ is known.* As already explained, two specimens showing two different angles β on the same bedding plane are sufficient to determine D and α with an accuracy which is only impaired by imperfections of the material. Some of the methods are described elsewhere (Sdzuy 1962); those described here are easier to use.

For a quick determination of D and α , the graph (text-fig. 3) may be used as follows: Measure the two angles β and angle γ , then find in the graph the curve representing D , on which the intersections with the horizontal lines representing the two angles β are separated on the horizontal scale by angle γ . One drawback to this method is that the measuring of the several angles is somewhat tedious; another is that because the curves representing D in the graph have been constructed at intervals of 5%, it is sometimes difficult to locate precisely the two points in the diagram which satisfy the observed angles.

The easiest way to determine the deformation in fossils is by making use of a device which allows direct reading of D and α_2 . Such a device is described in the following section.

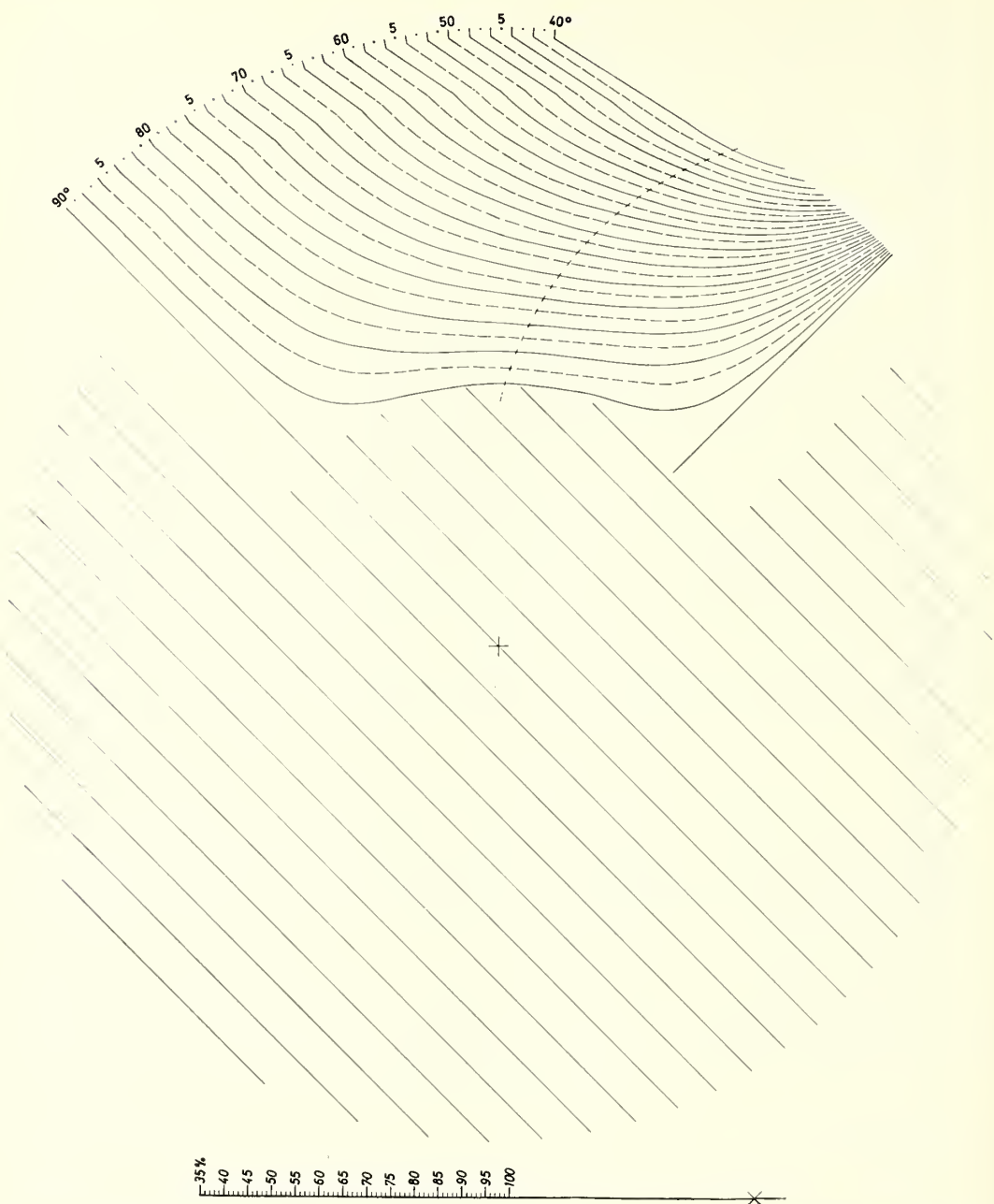
DEVICE FOR DIRECT READING OF D AND α_2

Description. The device is made of four discs of transparent material which can be rotated around their common centre (M in text-figs. 5, 6). Two of the discs (named A for convenience) bear the design shown in text-fig. 4: a set of parallel lines in the central part and a set of curves.

The other two discs (B) bear the following design: one line through the centre and a marker (m in text-figs. 5, 6). This marker has to be at a distance from the centre which is just a little greater than the distance of the outer margin of the curve-design in disc A from the centre. The connecting line between this marker and the centre of disc B must be at right angles to the line through the centre. The design of disc B is indicated in text-figs. 5 and 6.

In addition to discs A and B, a ruler is needed (text-figs. 4, 6), on the scale of which the amount of D is indicated. It is convenient to fix this ruler, also moveable, to the common centre of the four discs.

The most important and also the most complicated part of the device is the design in disc A. If one wishes to make a device as described here, one may do so by simply reproducing text-fig. 3 photographically and enlarging it to a convenient size on sheets of clear film. Care must be taken that the ruler (also shown in text-fig. 4) is reproduced at



TEXT-FIG. 4. Disc A and ruler. Both must be reproduced on exactly the same scale. The mode of construction of the curves in disc A is explained in text-fig. 5. The centre M is indicated by a cross in the central part of disc A and on the ruler. On the scale in disc A the number of degrees of the acute angle β will be indicated by the marker of disc B (the corresponding obtuse angle β equals $180 - \text{acute angle } \beta$; angle α_2 , as needed for the construction of the curves, is obtained by subtracting the acute angle β

exactly the same scale as disc A. The two sheets of film, corresponding to discs A, may then be placed between two plates of glass or some stiff transparent plastic, into which the simple design of disc B has been scratched. The ruler also can be made of transparent plastic. A small screw through the centre of the discs and through the ruler will hold them in place and allow them to rotate against each other.

Each of the curves in disc A represents for a given angle β the possible values of angle α_2 at deformations ranging from $D = 35\%$ to $D = 100\%$. The mode of construction of these curves is explained in text-fig. 5. The intersection of the two curves for two different angles β in their natural position (separated by angle γ) will then show the correct angles α_2 for the two deformed fossils.

Use of the device. 1. To determine D and α_2 from two specimens on one bedding plane, proceed as follows (see also text-fig. 6):

- a. Place the device over the bedding plane with two deformed specimens (or, better, over a photograph of the same on which the two angles β have been drawn with ink).
- b. Make the lines in the central part of one of the discs A parallel to the *right* side of one of the *acute* angles β (or to the left side of the corresponding obtuse angle β). The line in the central part of one of the discs B must be parallel to the *left* side of the same acute angle β . Do the same with the other two discs for the other angle β , without changing the position of the device.
- c. Follow the two curves indicated on the two discs A by the markers of the corresponding discs B to their point of intersection.
- d. Place the ruler over this point of intersection, so that the centre M of the ruler coincides with the centre of the discs. The direction of the ruler is then equal to the principal axes of strain, and the point of intersection of the two curves will indicate on the scale of the ruler the exact amount of deformation.

2. If Breddin's method has to be employed, only one pair of discs A and B is needed. Proceed as follows:

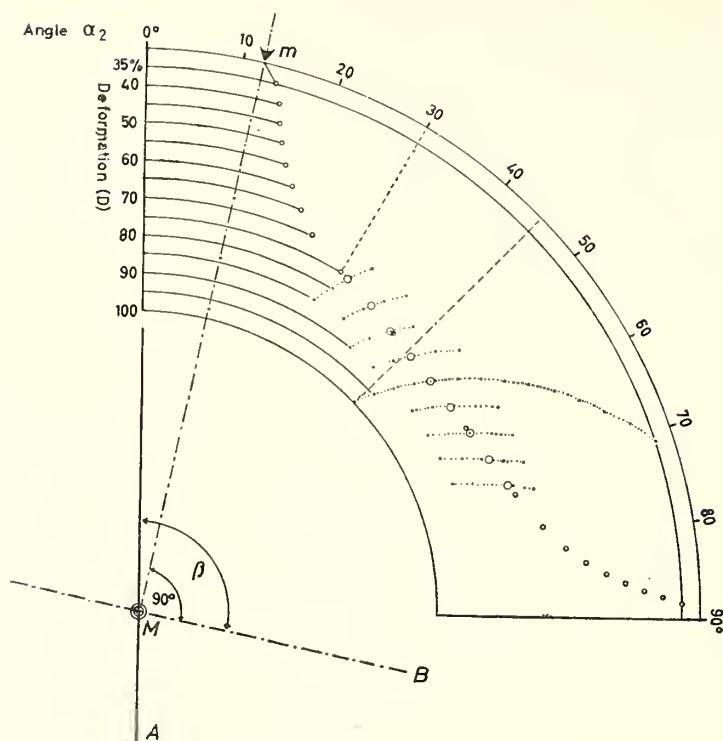
- a. To find the most deformed specimen, the device serves as a convenient angle meter; if the lines in the central parts of the discs are parallel to the sides of angle β , the marker of disc B will indicate the number of degrees on disc A.
- b. The point of intersection between the curve representing $\alpha_1 = 45^\circ$ on disc A and the curve of the most oblique angle β indicates the approximate value of D on the ruler (see text-fig. 7).

TEXT-FIG. 4 (*continued*)

from 90°). The dashed line cutting across the curves in disc A represents angle $\alpha_1 = 45^\circ$; it helps to find D by Breddin's method.

For the sake of clarity, only those curves corresponding to angles β with a round number of degrees have been drawn. To help avoid confusion of neighbouring curves, every second one has been drawn as a dashed line. The short radial part at the left end of each curve serves to connect the marker of the corresponding disc B with the curve. This radial part may be cut off in one of the two discs A needed and the marker of the corresponding disc B may be placed accordingly nearer to the centre of the disc; this will help to distinguish more easily the two superimposed sets of discs.

The set of parallel lines in the central part of disc A, which has to be parallel to the right side of the acute angle β , helps to measure specimens without rearranging the lines forming the two angles β .



TEXT-FIG. 5. Mode of construction of the curves in disc A, exemplified by the curve corresponding to angle $\beta = 102^\circ$. It is advisable to draw this on a polar stereographic net, as used in structural geology.

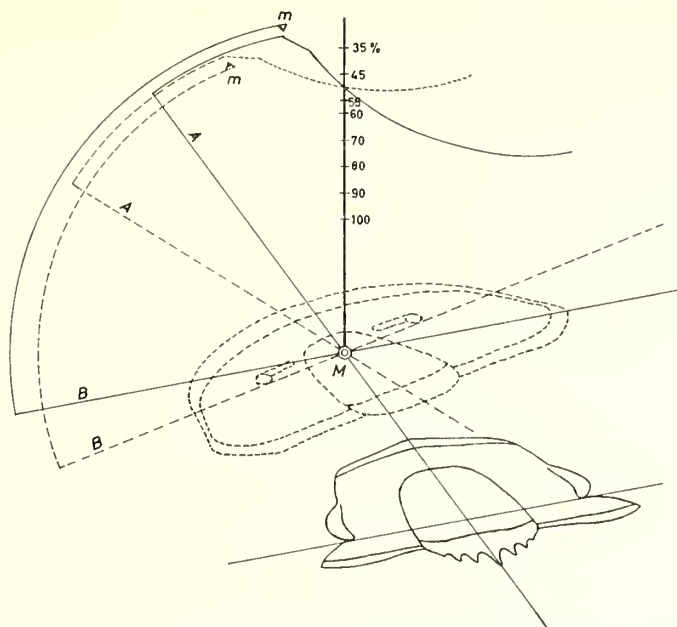
A net is formed by concentric lines, corresponding to degrees of deformation D (indicated only in the left side of the drawing), and by radii, corresponding to angle α_2 (indicated only for $\alpha_2 = 30^\circ$ and 45°). Into this net the horizontal line representing angle $\beta = 102^\circ$ in the graph, text-fig. 3, is transported. (For instance: in text-fig. 3, $\beta = 102^\circ$ intersects the curve representing $D = 75\%$ in the vertical line representing $\alpha_2 = 30^\circ$; the curve constructed in text-fig. 5 has therefore to intersect the concentric line representing $D = 75\%$ on the radius that corresponds to $\alpha_2 = 30^\circ$.) Points found in this manner are indicated by small circles.

Those points are sparse in the middle part of the curve. Additional points may be found here by transferring the lines representing the changes of angle α_1 from the graph, text-fig. 3, into the net (indicated by small points, all of them drawn for the line corresponding to $\alpha_1 = 45^\circ$ only). The points of intersection of those lines with the horizontal line representing angle β can then be transferred from the graph into the net. Points found in this manner are indicated by larger circles.

On the outer circumference, beyond the concentric line corresponding to $D = 35\%$, the intersection with the radius corresponding to angle $\alpha_2 = \beta - 90^\circ$ is marked. (Where $\beta = 102^\circ$ is chosen as example, this is the radius corresponding to $\alpha_2 = 12^\circ$.) This point is connected to the end of the curve which is on the concentric line corresponding to $D = 35\%$. This point will be aligned to the marker of disc B if the lines in the central parts of the two discs include the angle β , to which the curve corresponds.

The lines in the central part of disc A have to be parallel to the radius corresponding to $\alpha_2 = 0^\circ$.

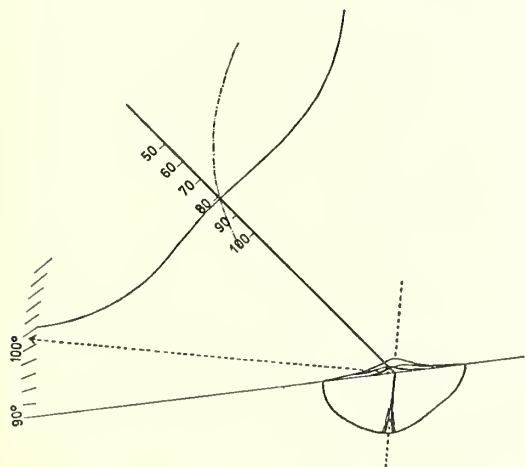
The design of disc B is indicated by dotted lines: a line, or a system of parallel lines, in the central part and a 'marker' (m) at right angles to it. (The thin line connecting M and m is not necessary on disc B; it has been drawn to show the position of m .) The lines in the central parts of discs A and B include an angle of 102° (or 78°), and consequently ' m ' is aligned with the starting point of the curve corresponding to $\beta = 102^\circ$ of disc A.



TEXT-FIG. 6. Use of the device to determine D and α_2 , exemplified by two distorted cranidia of trilobites.

One cranidium, its main axes forming angle β , and the elements of discs A and B corresponding to it, are drawn with dashed lines. The other cranidium and elements of the discs corresponding to it are drawn with full lines (one axis of this cranidium is transferred into M). The ruler is indicated by a heavy line.

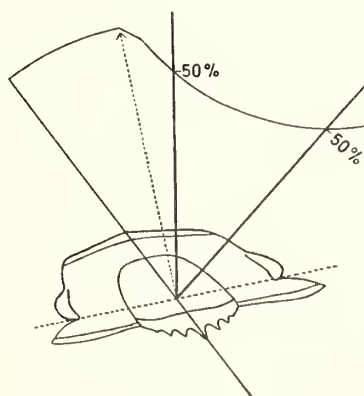
The lines in the central parts of discs A and B (indicated by letters in the drawing) are parallel to the axes of the fossils. The markers 'm' of the two discs B indicate a curve each on the corresponding disc A. The point of intersection of the two curves indicates on the ruler a deformation of 50%; the ruler, placed over the point of intersection, is parallel to the direction of deformation. Distortion of the two fossils in text-fig. 5 would be eliminated after stretching them to twice their extent parallel to the direction of the ruler.



TEXT-FIG. 7

TEXT-FIG. 7. Determination of D with specimen in which angle β is most strongly deformed (indicated by a brachiopod). See text. Angle β of the specimen is 102° (or 78°); D is then about 81%, as can be read on the ruler.

TEXT-FIG. 8. Distorted fossil. D is known (50% in this case). Two different positions of the ruler are possible; one of them is parallel to the direction of principal strain. The marker of disc B is indicated by an arrow in text-figs. 7 and 8.



TEXT-FIG. 8

3. If D is known, α_2 can be found in any single specimen as follows (see also text-fig. 8):

- a. Make the lines in the central parts of a single pair of discs A and B parallel to the sides of angle β .
- b. The point on the ruler corresponding to D is then placed on the curve of disc A indicated by the marker. Of the two different positions of the ruler, one is parallel to the direction of deformation.

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ON *BIRGERIA ACUMINATA* AND THE ABSENCE OF LABYRINTHODONTS FROM THE RHAETIC

by R. J. G. SAVAGE and N. F. LARGE

ABSTRACT. A maxilla of *Birgeria acuminata* from the Rhaetic of the Bristol Channel is described. Previous records of labyrinthodonts from the British Rhaetic are shown to belong to this piscine genus.

VERTEBRATE remains from the Rhaetic Bone Bed around the Bristol Channel are well known. The great majority of the small specimens comprise fish teeth, scales, and spines while the larger specimens are attributable to reptiles, mainly plesiosaurs and ichthyosaurs. The fish remains usually figure under the names *Acrodus*, *Hybodus*, '*Saurichthys*', *Nemacanthus*, *Sargodon*, *Gyrolepis*, and *Ceratodus*. In addition to the marine reptiles, *Plesiosaurus* and *Ichthyosaurus*, occasional terrestrial reptiles have been found; these bones have been referred to dinosaurs but the material is not sufficiently diagnostic for more precise identification. From specimens which have been described and from material now in the University of Bristol Geology Museum, at least two species of terrestrial reptile are clearly represented, a large species and a small species about 2–3 ft. long. No pterosaurs or mammals are recorded from the Bone Bed, and there remains for consideration only one other vertebrate group, the amphibia.

Miall (1875) reported that *Metopias diagnosticus* von Meyer, a labyrinthodont from the Keuper of Germany, was present in the Aust Bone Bed and the statement has been often repeated in the literature. Reynolds (1946) stated that labyrinthodont remains were common at Aust, usually very fragmentary cranial bones with 'characteristic' pitted surface and rarely jaw fragments with teeth. Reynolds further noted that two types of teeth are found on these jaw fragments, and that some isolated teeth commonly attributed to *Saurichthys* may be labyrinthodont.

The true identity of these 'labyrinthodont' specimens has remained unresolved, due largely to lack of really good material. Reynolds illustrated a mandible fragment with five teeth, but the specimen is highly pyritized and impossible to prepare. In 1954 Professor C. F. A. Pantin found a dentary which he kindly donated to the University of Bristol Geology Museum (UBGM 19001); this specimen prepared well in acetic acid and has four teeth. More recently one of us (N.F.L.) found a maxilla at Westbury-on-Severn which contains seven major teeth and a labial row of smaller teeth. The specimen has been beautifully prepared by Mr. A. E. Rixon of the British Museum (Natural History) and is described in detail below; it is patently *Birgeria* and indistinguishable from other specimens previously referred to the labyrinthodonts, which can now be placed in this piscine genus.

Family BIRGERIIDAE Berg 1940

Diagnosis. Body almost naked, scales only present on dorsal half of caudal pedicle, on body axis of caudal fin, and anteriorly to the caudal pedicle in a single row along the main lateral line. As in the Palaeoniscidae, two nasal openings on each side, one anterior

and one posterior to the postrostral. Sensory canal system differing from that in Palaeoniscidae mainly in the following respects: supraorbital sensory canal ending blindly in rostromaxillary without communicating with ethmoidal commissure of infraorbital sensory canals; dorsal part of preopercular sensory canal extending from radiation centre of preoperculum in an almost anterior direction towards most dorsal part of postorbital vertical section of infraorbital sensory canal. Very large unpaired rostromaxillary. Parietals (one or two on each side) separated by frontals. One (or two?) extrascapulars on each side. Supratemporal independent. Intertemporal fused with dermosphenotic and with a number of posterior supraorbitals. A larger or smaller number of free supraorbitals. Neural endocranium not ossified in a single piece but in separate bones (an unpaired occipital bone, a paired prootic-opisthotic, a paired autosphenotic, an unpaired sphenoid, and a paired ethmoidal bone). Posterior myodome smaller than in Palaeoniscidae. Parasphenoid strong, extending backward below the whole neural endocranium, and with a strong paired processus ascendens. Mouth much larger than in Palaeoniscidae. Suspensorium very oblique. Teeth on jaws arranged in a labial and a lingual row. Labial teeth small, lingual teeth very large. Operculum small, suboperculum lobate much as in *Polyodon*. Spiracle present. Branchiostegal rays numerous. Fin rays jointed, devoid of ganoine. Pelvic fin large, with about fifty lepidotrichia. Dorsal and anal fins both situated far back, dorsal fin slightly anterior to anal fin, both fins large and with more than fifty lepidotrichia. Fulcra present only on the body axis of the caudal fin. Endoskeleton of dorsal fin represented by three series of radial ossifications; an axonost, a baseost, and a distal series. Endoskeleton of anal fin represented by two series of radial ossifications, probably an axonost and a baseost series; baseost series very short, supporting only posterior third of fin. Posterior elements of axonost series of endoskeleton of both dorsal and anal fins fused to a fairly extensive axonost plate. Notochord persistent. Axial skeleton with ossified dorsal and ventral arcuals, in abdominal region moreover with supraneurals, in part of caudal region possibly also with independent infrahaemals. Skeleton of pelvic fin consisting of an ossified pelvic plate and one or two rows of radial ossifications.

Remarks. The family name was erected by Aldinger (1937) but without a diagnosis. Nielson (1949) gave the above detailed amended diagnosis in the light of new Greenland Triassic material. Nielsen bases the family on *Birgeria* and does not definitely include in it any other genus.

Genus *BIRGERIA* Stensiö 1919

Diagnosis. Large or fairly large fishes. Trunk long and slender, oval in transverse section. Head rather large, with big eyes and extremely long jaws. Neural endocranium narrow both anteriorly and posteriorly, but very broad in its middle part and especially between its strong postorbital processes. Neural endocranium in both small and large specimens partly occupied by a number of independent bones. External dermal bones of the head relatively thick and mainly ornamented with tubercles, to a smaller extent, however, also with striae. Striae best developed on maxillary and dentalo-splénial, and on these bones to some extent covered by more superficially situated tubercles of varying shape. On the jaws a labial row of small, and a lingual row of large teeth. Parallel with these two rows, a third row consisting of small to medium-sized teeth on the ventral or ventro-

lateral part of the oral faces of the ectopterygoid and the dermopalatines. Moreover, large areas of oral faces of ectopterygoid, entopterygoid, dermopalatines, dermo-metapterygoid, and prearticular covered by very small teeth. Small teeth also present on ossifications of basibranchial series and branchial arches. Teeth of jaws and at least larger teeth on dermal bones of palate pointed and conical with a two-edged enamel cap, in the geologically older species on the whole smooth, in the geologically youngest species equipped with vertical, elevated, sharp striae; basally to enamel cap the teeth of all the species vertically striated, either with fine striae alone or with coarse striae which in their turn bear the fine striae; plicidentine not present. Teeth of branchial arches more slender than those of the jaws and with an enamel cap, which always seems to be smooth. [Abbreviated from Nielsen 1949, pp. 280–4.]

Type species. *Birgeria mougeoti* (Ag.) from the Triassic of Europe and Spitsbergen.

Species. In addition to the type species, the following species have been recognized by Nielsen as belonging to the genus:

<i>Birgeria stensiöi</i> Aldinger 1931	from Triassic of Europe
<i>Birgeria groenlandica</i> Stensiö 1932	from Triassic of Greenland
<i>Birgeria velox</i> (Jordan) 1907	from Triassic of California
<i>Birgeria acuminata</i> (Ag.) 1844	from Rhaetic of Europe
<i>Birgeria costata</i> (Münster) 1839	from Rhaetic of Europe
<i>Birgeria annulata</i> (Winkler) 1880	from Triassic of Europe
<i>Birgeria nielseni</i> Lehman 1948	from Triassic of Madagascar

Remarks. The diagnosis in Nielsen (1949, pp. 280–4) contains an account of the anatomy of the genus. It has been shortened here to the statements apposite to the present discussion. Lehman (1952) gives a full synonymy for the genus. Although eight species are listed, most are poorly known. They have a wide geographic distribution and relatively narrow stratigraphical range from the Lower Triassic to the Rhaetic.

Birgeria acuminata (Agassiz)

Plate 20

Abbreviated Synonymy.

- 1843 *Saurichthys apicalis*, J. E. Portlock (*errore*), p. 470, pl. 14, fig. 19.
- 1844 *Saurichthys acuminatus*, L. Agassiz, p. 86, pl. 55a, figs. 1–5.
- 1844 *Saurichthys longidens*, L. Agassiz, p. 87, pl. 55a, figs. 17, 18.
- 1921 *Birgeria acuminatus*, E. A. Stensiö, p. 150.

Remarks on the Synonymy. Without a detailed study of the German material it would be pointless and possibly confusing to list the twelve specific names sometimes ascribed to *Saurichthys*, among which some are probably synonymous with *B. acuminata*. Details of these are to be found in Woodward (1895, pp. 21–23) and Boni (1937).

Diagnosis. Large fish with robust dentition. Basal portion of teeth below enamel cap relatively shorter than in *B. mougeoti*. Enamel cap terminated proximally by prominent collar; teeth with fine vertical striations, best developed immediately proximal to collar.

Remarks on Diagnosis. Agassiz (1844) noted the dental characters which differentiate *B. mougeoti* from *B. acuminata*. Woodward (1895) restated some of these. Boni (1937, pp. 584–5) listed characters including table of jaw lengths, which he regarded as

differentiating *B. mougeoti*, *B. stensiöi*, *B. groenlandica*, and *B. acuminata*. Lehman (1952) stated that *B. groenlandica* had two forms, a large and a small, the latter being comparable with *B. nielsenii*. Boni (1937, p. 596) in discussing *B. costata* from the Rhaetic of the Imagna Valley in Italy, suggested that presence or absence of a keel on the tooth crown is a variable which cannot be relied upon as a specific character. *B. costata* is very much larger than *B. acuminata*. Stratigraphically only *B. acuminata* and *B. costata* among *Birgeria* species have a Rhaetic range; whether these are merely stratigraphic species or represent biological differences must await better material. *B. acuminata* is common in the Rhaetic of north-west Europe and there are no known occurrences outside the Rhaetic.

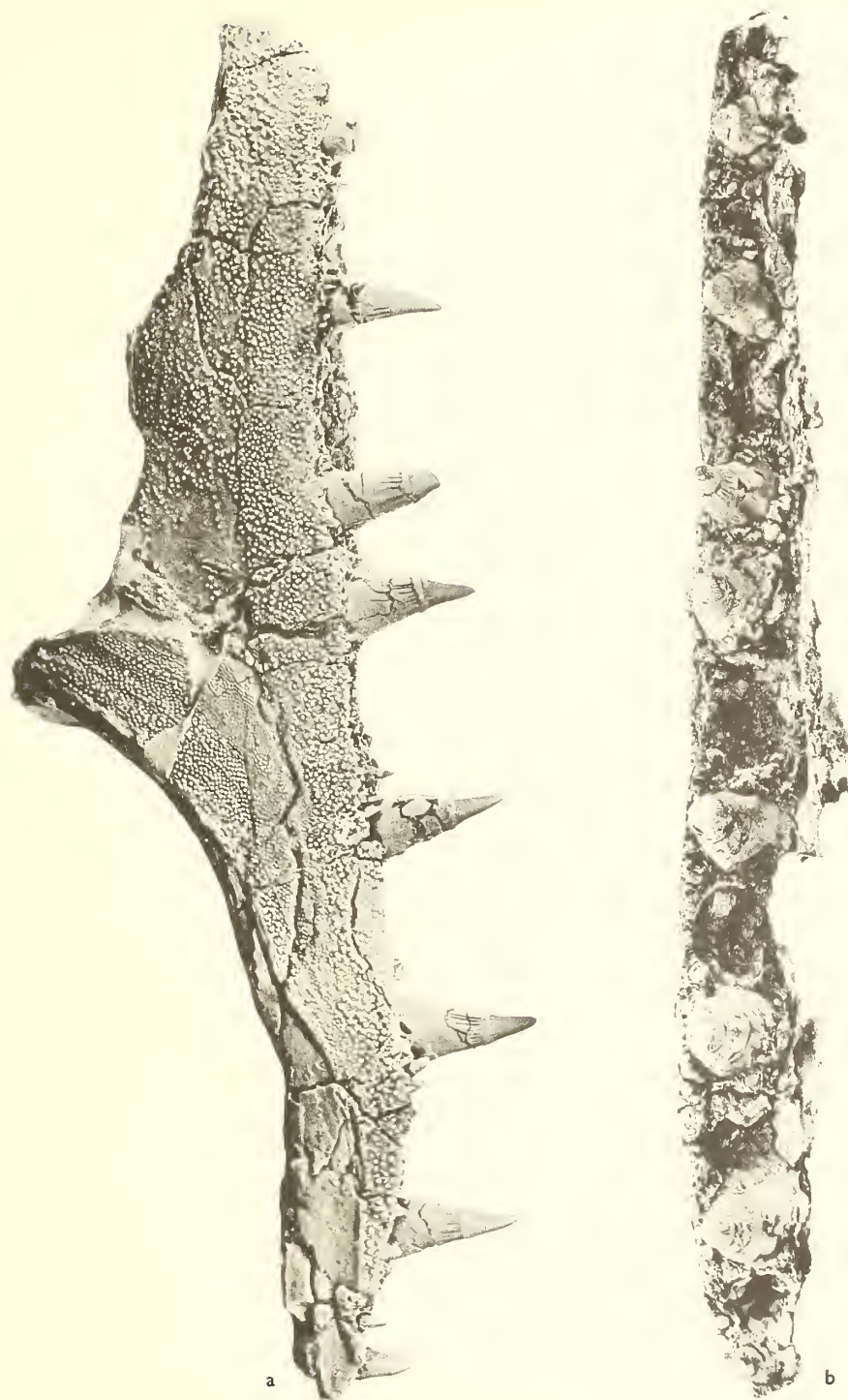
Holotype. The teeth illustrated by L. Agassiz (1844) on Plate 55, figs. 1–5 were described by him as coming from the Muschelkalk of Aust Cliff. The specimens, then in the Bristol Institution Museum, were later incorporated in the Bristol City Museum collections and registered collectively under the catalogue number C 4578. Unfortunately all were destroyed when the Museum was bombed in 1941. The horizon is undoubtedly the Rhaetic Bone Bed at Aust Cliff, 10 miles on 6° west of north from Bristol (NGR 566898). The International Rules of Zoological Nomenclature do not encourage the creation of neotypes unless circumstances are exceptional and to conform to this ruling no new type is here established.

Description. The new specimen of *Birgeria acuminata*, BMNH P47287, is from the Westbury Shales of the Rhaetic at Westbury-on-Severn, 8 miles WSW. of Gloucester, (NGR 715132). The specimen comprises the middle portion of a left maxilla, and is broken both anteriorly and posteriorly while the dorsal ramus is largely missing. The external surface is completely covered with fine tubercles except along the antero-dorsal margin where the orbital bones overlapped. The tubercles are densest along the dental margin and near to the orbital region are extremely fine. The dorsal part of the bone is insufficiently preserved to detect any pattern in the arrangement of the tubercles. Internally the bone is smooth and extended along the ventral margin of the teeth.

Along the 12 cm. of tooth row preserved there are 14 alveoli for lingual teeth and in 8 of these the teeth are present. Lateral to these the maxilla margin carries a row of small labial teeth, of which some 8 remain intact. The lingual teeth are conical, lie close together in a row without any space between them at the level of the insertion into the maxillary bone. When a tooth is missing an ovoid pit remains which extends on either side to the base of the adjoining teeth. At the level of the ventro-lateral maxillary margin the lingual teeth appear more spaced due to the effect of the tapering cone and the distance between the teeth is about equal to the tooth diameter at this level. The ventro-lateral margin of the bone varies in thickness a little; is thickest between the lingual teeth and thinnest around them. The distribution of the labial teeth is slightly irregular, but the pattern is broadly a single row with on average 6 labial teeth to every one lingual tooth. In size the labial teeth tend to be slightly larger between the linguals and smallest when alongside the linguals. The lingual teeth also vary slightly in size, but without any observable pattern; their size may reflect more the time of eruption than their position in the jaw.

EXPLANATION OF PLATE 20

Birgeria acuminata (Agassiz), UBG M 19001, Rhaetic of Westbury-on-Severn, Gloucs. Left maxilla *a*, lateral aspect; *b*, occlusal aspect. $\times 1.5$.



SAVAGE and LARGE, *Birgeria acuminata* from the Rhaetic

The lingual teeth are roughly conical in outline, the basal portion being flayed out for attachment to the bone. The conical axis of the teeth is curved slightly inward, but there is no detectable anterior or posterior curvature. Each tooth is terminated by an enamel cap, which in newly erupted teeth is pointed but becomes blunted with wear. The tooth cap is terminated proximally by a ring, collar, or cingulum. From this collar arise anterior and posterior keels which do not quite reach the summit. Fine striations also arise from the level of the collar, and extend both proximally and distally; they are densest on the medial side of the tooth and are few or lacking on the lateral side. Those rising on to the cap do not reach the summit and frequently unite. Those extending proximally also disappear before reaching the base. The labial teeth appear to have a similar build to the linguals though striations and keels are rarely detectable.

Remarks. The purpose of the present paper is to clear up some of the confusion prevailing with respect to labyrinthodonts in the Rhaetic and a detailed appraisal of *Birgeria* is not attempted. The Westbury beds of the Rhaetic yield vertebrates at several horizons, from the shales and limestones as well as from the basal bone conglomerate. The vertebrate fauna appears to be essentially the same at all levels though reptile bones are rare outside the basal bone bed. Isolated conical teeth are abundant in the Westbury beds and these can invariably be assigned to either *Birgeria* or *Ichthyosaurus*. The *Ichthyosaurus* teeth differ from those of *Birgeria* in being larger, less tapering and hence more nearly parallel sided, and in lacking a collar; keels on the caps are wanting and the proximal portion of the teeth is infolded to a greater or lesser extent. While most teeth are recognizable on external morphology, preliminary investigations suggest that histological structure can be used to distinguish reptile and fish, and possibly even to identify genera. Careful collecting from individual beds and use of histological techniques could considerably advance our knowledge of these faunas.

Several other maxillae and mandibles are known beside the specimen described above; though none is so well preserved they are all clearly *Birgeria* and not labyrinthodont. Reynolds (1946) described a mandible (UBGM 7976) as '*Metopias diagnosticus*'; the specimen is unfortunately highly pyritized and cannot be prepared with acid, but is undoubtedly *Birgeria acuminata*. Woodward (1889) described a left maxilla (BCM C4579) as *Saurichthys acuminatus*; the specimen is closely comparable with that described above, has two lingual teeth and the row of alveoli for the labial teeth is distinguishable. Numerous other smaller pieces of maxilla and mandible exist in collections. Another frequently found part is the symphysis of the mandible; this is very thick and heavy (e.g. UBGM 18038, i-iv). Comparison of *Birgeria* with the living *Lepidosteus* is particularly close on many anatomical features—the long jaws, the heavy mandibular symphysis, the external ornament, the arrangements of the lingual and labial teeth; striations and keel are present on the lingual teeth but differ in detail from those of *Birgeria*.

A search of the Rhaetic exposures around the Bristol Channel and museum collections has revealed no vertebrate material that cannot be assigned to either fish or reptile. The previous records of 'labyrinthodont' are shown to be misidentifications for large specimens of *Birgeria*. No evidence for amphibia remains. Stratigraphically this interpretation clarifies the position regarding the labyrinthodonts. It can now be stated that there are no known Rhaetic metaposaurid labyrinthodonts; their last appearance is in

the Upper Triassic beds of India and North America. Jain, Robinson, and Roy Chowdhury (1964) record metaposaurs from the Maleri beds of the Pranhita-Godavari valley, India, and these beds they equate with the Carnian to Middle Norian zones of the marine Upper Triassic.

Nilsson (1946) recorded the presence of a plagiosaur from the Rhaetic of Scania, Sweden; the material he identified as *Gerrothorax* and is well preserved in a coal-bearing deposit of Middle Rhaetic age. Nilsson considered the plagiosaurs to form the type family of an order of Triassic stegocephalians, distinct from labyrinthodonts. Panchen (1959) writing on plagiosaur affinities, excluded the brachyopids from his order Plagiosauria and placed the plagiosaurs within the superorder Labyrinthodontia. Hence the presence or absence of labyrinthodonts in deposits of post-Triassic age depends on (a) whether the definition of the Labyrinthodontia includes or excludes the Plagiosauria and (b) whether the definition of the Trias includes or excludes the Rhaetic. The Rhaetic of Britain has yielded no amphibia; the Rhaetic elsewhere contains amphibia which may be labyrinthodont.

Acknowledgements. We have had discussions and correspondence with the late Professor B. Peyer, Dr. J. Griffith, Dr. D. Rayner, Dr. T. K. Roy Chowdhury, and Dr. B. Schaeffer; we are particularly grateful to Mr. A. E. Rixon for preparing the fragile specimen. Through the paper the following abbreviations for museums have been used: BCM, Bristol City Museum; BMNH, British Museum (Natural History); UBGM, University of Bristol, Geology Museum.

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THE UPPER DEVONIAN GASTROPOD *ORECOPIA* IN WESTERN CANADA

by A. E. H. PEDDER

ABSTRACT. The distribution of *Orecoxia* is reviewed. Apart from a possible Famennian occurrence in Nevada, the genus as presently known is confined to the Frasnian of western North America and eastern Europe and is represented by five described species. *Orecoxia mccoysi* and *O. uehtensis* are refigured and a new species, *O. cotei*, is erected for specimens from British Columbia and the Northwest Territories.

It is suggested that the Tathlina Formation of the southern Northwest Territories may be late, rather than middle Frasnian.

GASTROPODS now referred to *Orecoxia* have been known from Timan and Latvia since 1846 and from Nevada since 1884. Although subsequently numerous specimens have been identified from eastern Europe and cordilleran U.S.A., the genus has only once been reported in Canada, and then without either geographical or stratigraphical location. The present paper confirms that *Orecoxia* is present in Canada and describes a new species of late Frasnian age from British Columbia and the Northwest Territories.

Acknowledgements. It is a pleasure to acknowledge help extended from several sources. E. G. Kauffman and E. L. Yochelson of the United States National Museum arranged for the loan of specimens from Nevada, California, Latvia, and Timan, while further specimens from Nevada were provided by R. H. Wainess of the State University College, New Paltz. The Canadian specimens were collected during field-work mounted by Triad Oil Co. Ltd., Calgary. The management of the Company has granted permission to publish this work and has allowed the Company's specimens to be transferred to the Geological Survey of Canada, Ottawa.

SYSTEMATIC PALAEONTOLOGY

The collections containing types are abbreviated as follows:

GSC Geological Survey of Canada, Ottawa.
USNM United States National Museum, Washington.

Family OMPHALOTROCHIDAE Knight
Genus ORECOPIA Knight 1945

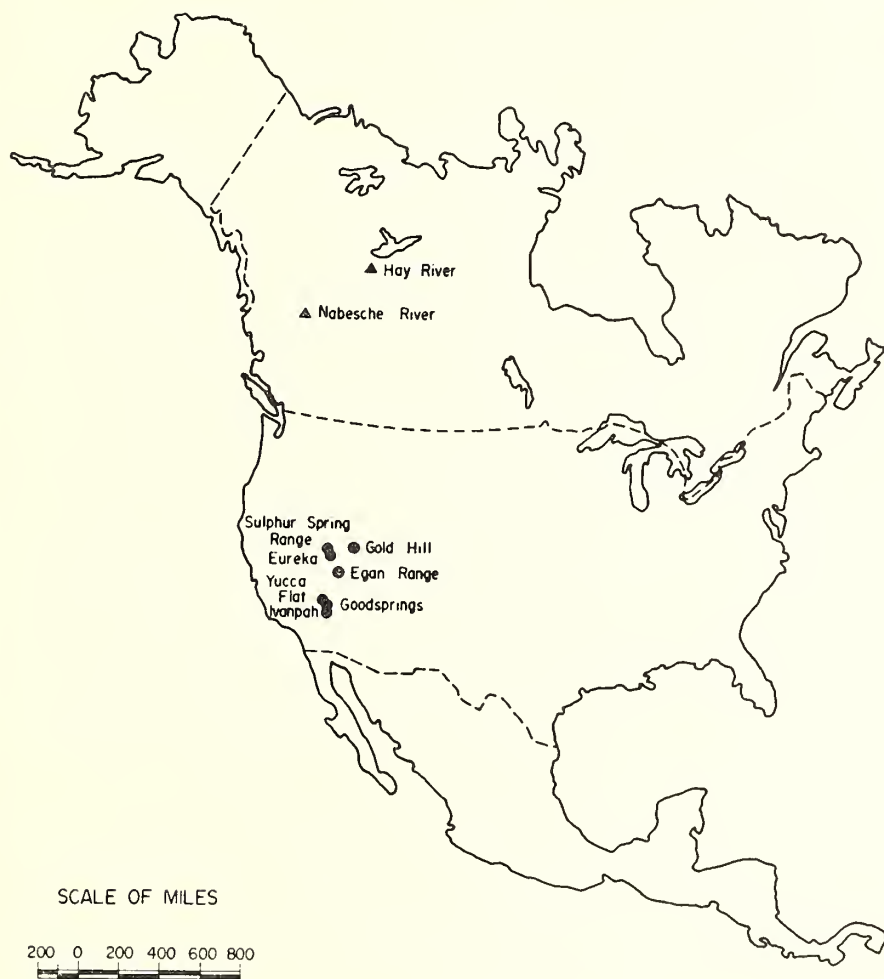
Type species (original designation). *Platyschisma? mccoysi* Walcott 1884, p. 188, pl. 17, fig. 1. 'Central portion of the Devonian limestone; Newark Mountain Eureka District, Nevada.' In terms of current stratigraphical nomenclature the type horizon probably lies in the upper part of the Hayes Canyon Member of the Devils Gate Limestone (Nolan *et al.* 1956) and is early Frasnian. Merriam (1940, pl. 11, fig. 3) has subsequently figured one of the syntypes and Knight (1945, pl. 80, fig. 1a-d, g) has figured the specimen, which he designated as lectotype, and also three paralectotypes.

Diagnosis. See Knight 1945, p. 586.

Distribution. At the present time five Frasnian species, including *Orecoxia cotei*, described below, are referred to the genus. These are distributed in western North America from southern California to Great Slave Lake and in the Soviet Union from Timan and Latvia

to the Urals. In addition one of the species may be represented by derived fossils from the North German Plain (Roemer 1885, p. 384, pl. 11, fig. 1a).

Orecoxia mccoysi (Walcott) and comparable forms are widely distributed in the Basin and Range Province of western United States. They have been reported in the higher parts of the Devils Gate Limestone in the Sulphur Springs Range (Carlisle *et al.* 1957,



TEXT-FIG. 1. Known distribution of *Orecoxia* in North America. Occurrences of *Orecoxia mccoysi* (Walcott) indicated by a circle and those of *Orecoxia cotei* sp. nov. by a triangle.

p. 2188), the *Phillipsastrea* Zone and Hayes Canyon Member of the Devils Gate Formation of the Eureka district (Merriam 1940, p. 60; Nolan *et al.* 1956, p. 51), the upper beds of the Guilmette Formation of the Gold Hill mining district (E. Kirk in Nolan 1935, p. 21), the upper member of the same formation in the southern Egan Range (Kellog 1963, p. 699), Devils Gate or Sultan equivalent in the Yucca Flat district (Johnson and Hibbard 1957, p. 356), the Valentine Member of the Sultan Formation

in the Spring Mountains of the Goodsprings Quadrangle (E. Kirk *in* Hewett 1931, p. 16; Knight 1945, p. 586 and collections made by R. H. Wainnes), and in the same formation in the Ivanpah Quadrangle (collected by Hewett, USNM loc. 2220). It is also possible that the species occurs in the upper beds of the Lost Burro Formation of the Ubehebe and Inyo Mountains of California (Merriam 1963*a*, p. 55; 1963*b*, p. 16). In view of the considerable morphological variation in specimens of *Oreocopia* from the Basin and Range Province, particularly in regard to the height of the spire and umbilical width, it is possible that more than one species is represented. Most occurrences are in the early Frasnian *argentarius* Zone and Merriam (1963*a*, p. 55) regards the gastropod as an especially useful indicator of the lower part of the zone. However, he previously reported (1940, p. 60) a comparable species in the slightly younger *Phillipsastrea* Zone northwest of Eureka, and there are sufficient Lime Creek species in the Valentine Member of the Sultan Limestone in the Goodsprings Quadrangle (E. Kirk *in* Hewett 1931, p. 16), to suggest that *O. mccoysi* may range into the Middle Frasnian.

Knight (1945, p. 586) alluded to undescribed specimens of *Oreocopia* from the Devonian of western Canada, but gave no information concerning their occurrence. Neither Dr. Kauffman nor Dr. Yochelson (personal communication, October 1963) has been successful in locating the material to which Knight was referring. The present paper describes *Oreocopia* from north-eastern British Columbia and south-western Northwest Territories and apart from Knight's paper, is the first report of the genus in Canada. Although there is no doubt that the first of these occurrences is late Frasnian, the second, in the Tathlina Formation, is less clearly dated. McLaren (1962, fig. 1) and the writer (*in* House and Pedder 1963, text-fig. 2) have placed the Tathlina Formation high in the middle Frasnian. The upper beds of the underlying Twin Falls Formation contain several species, including *Mictophyllum modicum* Smith, *Thamnophyllum tructense* (McLaren), and *Atrypa ciliipes* Crickmay, which are otherwise known only in the late Frasnian. Their presence below the Tathlina Formation and the presence of *Oreocopia cotei* in it are probably significant and suggest that the Tathlina Formation is late, rather than Middle Frasnian. In this case the *albertensis* Zone would be equivalent to the Twin Falls Formation only, of the Hay River sequence, and the Tathlina would correlate with part of the Nisku and Arcs Dolomites of Alberta.

Three species from the Soviet Union are now referred to *Oreocopia*. *Platyschisma uchtensis*, the first of these, was described by Keyserling (1846, pp. 263, 264, pl. 11, fig. 6) and was said to occur in Devonian calcareous sandstone on the River Uchta (Ukhta), a tributary of the Ishma. In the light of Nalivkin's work (1947, p. 14) the type horizon is probably in either the Sirachoy or Ukhta Series and is late Frasnian. Tschernyschew (1884, p. 53, pl. 1, fig. 2; 1887, p. 35, pl. 5, fig. 4) extended the known geographical range of the species by describing specimens from the Voronezh and southern West Urals regions; in both areas these specimens were associated with '*Spirifer*' *anosofi* and would now be regarded as late Frasnian. Besides reiterating these occurrences Nalivkin (1947, pp. 9–21) reported the species in the Semiluki Formation of the Voronezh region, the Svinord, Ilmen and Buregi Formations of the Main Devonian Field and in the Kultuban Limestone of the southern Urals. Nalivkin regarded all these formations as middle Frasnian. However, Malakhova (1960; 1961) has shown that the foraminifera of the Kultuban Formation at Lake Kultuban indicate that the formation includes both younger and older beds.

Platyschisma kirchholmiensis, the second of Keyserling's (1846, p. 264, pl. 11, fig. 7) species now referred to *Orecoxia*, came from the Düna (Zap Dvina) River, near Kirchholm, in Livland (Latvia). Keyserling considered the age of *P. uchtensis* and *P. kirchholmiensis* to be 'analagous'. Stuckenberg (1878, pp. 469, 470) placed *Rotella microstoma* Eichwald (1860, p. 1163) in synonymy with *P. kirchholmiensis* and claimed a wide distribution for the species in the southern part of the main Devonian Field and in the Voronezh region. Little is published concerning the exact horizon of these occurrences, but it seems likely from Pacht's (1859) and other work that the species is middle Frasnian in the type region.

Without access to specimens, the generic identity of *Platyschisma? ambiguum* (Walcott 1884, pp. 188, 189, pl. 17, fig. 3) remains in doubt. Walcott regarded it as congeneric with the type species of *Orecoxia*, but the species was not mentioned by Knight in his discussion of the genus. It was originally cited as coming from the 'upper horizon of the Devonian limestone, The Gate, Eureka District'. The wording suggests that the type horizon is in the 'Cyrtospirifer' Zone of the Devils Gate Formation (Merriam 1940, p. 51). This zone is a correlative of the Alexo and Sassenach Formations of Alberta and is early Famennian, consequently if *P. ambiguum* is an *Orecoxia*, it would be the youngest of the species ascribed to the genus.

Orecoxia cotei sp. nov.

Plate 21, figs. 2, 6-9, 11, 12, 14; text-fig. 2b

Name derivation. From L. F. Cote.

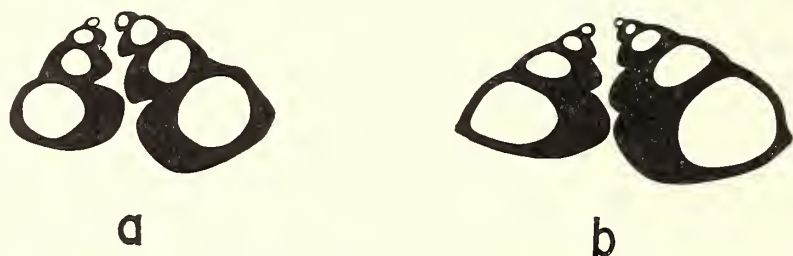
Material. Holotype, GSC 17633; paratypes 1-3, GSC 17634-6 respectively. The holotype and paratypes 1, 2 were collected by L. F. Cote in 1959 from an unnamed grey, medium-grained limestone, 140 ft. below the Besa River Formation, near Nabesche River, British Columbia, lat. 56° 17' N., long. 123° 23½' W. The gastropods were accompanied by a typical late Frasnian assemblage including *Phillipsastrea exigua* sensu Smith 1945 non Lambe 1901, *P. vesiculosa* Smith, *Hexagonaria* sp., *Thamniophyllum* sp., 'Ptychophyllum' *kindlei* Smith, *Thamniopora* sp., *Devonoproductus* sp., *Atrypa* sp., *Spinatrypa* sp., and *Theodossia* or *Vandergrachtella* sp. From small collections made 905 and 955 ft. lower in the same section, D. J. McLaren has identified the early Frasnian rhynchonelloid *Leiorhynchus russelli* McLaren.

Paratype 3 was collected by the author in 1958 from the Tathlina Formation on Hay River, opposite mile 59.1 of the original Mackenzie Highway, Northwest Territories. It occurred in a fawn, fine-grained limestone containing fine detrital quartz and was accompanied by *Nervostrophia* sp., *Devonoproductus* sp., *Atrypa ciliipes* Crickmay, *Atrypa* sp., *Tenticospirifer* sp., and *Theodossia* or *Vandergrachtella* sp. As discussed above, the precise age of the fauna is in doubt, but is either late Middle, or early Late Frasnian.

Diagnosis. Umboniform species of *Orecoxia* having a mean spire angle of about 110°. Periphery low in the whorl section and carinate. Growth-lines with a very marked forward projection at the periphery.

Description. Shell umboniform, having a mean spire angle of about 110° after the formation of five whorls. In early stages the umbilicus is relatively wide, but is reduced during growth, so that the shell is narrowly, or even minutely phaneromphalus in late stages. Protoconch unknown. Sutures very shallow. The whorl section is gently arched from the suture to the periphery and immediately under the periphery, but is almost

flat along much of the base; the periphery is marked by a distinct, although variable carina; the adaxial region of later whorls is apparently much thickened, however the interior of the sectioned paratype is poorly preserved, and the later whorls in text-fig. 2b are liberally reconstructed in the adaxial region. Growth-lines are re-entrant below the suture giving rise to a broad asymmetrical sinus on the upper abaxial surface of the whorl. Towards the periphery they project forward prominently, but immediately under



TEXT-FIG. 2. Cross-sections of *Orecopia*. Both $\times 2$. a. *Orecopia mccoysi* (Walcott), GSC 17638. Collected by R. H. Wainnes from the Sultan Formation in the Spring Mountains, Goodsprings Quadrangle, southern Nevada. b. *Orecopia cotei* sp. nov., paratype 1, GSC 17634. Unnamed late Frasnian limestone, 140 ft. below base of the Besa River Formation, near Nabesche River, British Columbia.

the periphery are abruptly swept back again; another more gentle projection is present near the umbilicus; thus over the base the growth-lines are sigmoidal. The largest specimens seen have about five whorls and are between 20 and 25 mm. in diameter and between 10 and 12 mm. high.

Comparisons. The new species resembles *Orecopia uchtensis* more than *O. kirchholmiensis* or *O. mccoysi*. The spire angle is similar in both species, but the whorl profile and growth-lines are different; in *O. cotei* the periphery is more acute and carinate, is also nearer the base, and the forward projection of the growth-line at the periphery is much more pronounced.

Orecopia kirchholmiensis has a higher spire and more rounded whorl periphery.

Most specimens of *Orecopia mccoysi* differ considerably from the new species by having a much higher spire, deeper sutures, and a well-marked angulation on the upper abaxial surface. The specimen shown in text-fig. 2a is a low-spired example of *O. mccoysi* and yet the mean spire angle of about 95° is distinctly less than that of *O. cotei*.

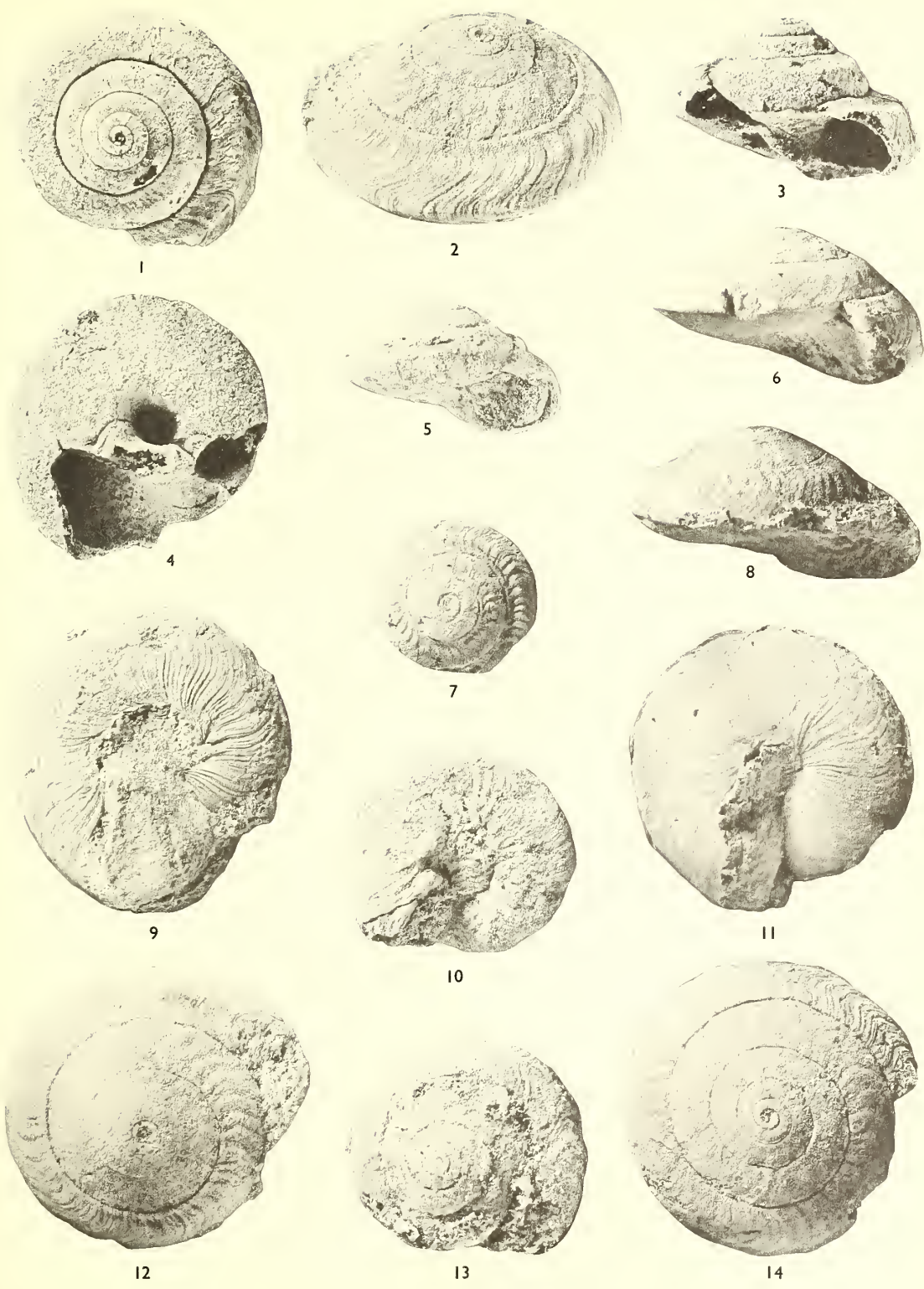
EXPLANATION OF PLATE 21

All figures $\times 2$.

Figs. 1, 3, 4. *Orecopia mccoysi* (Walcott). GSC 17637, collected by R. H. Wainnes from the Sultan Formation (early or middle Frasnian), Spring Mountains, Goodsprings Quadrangle, southern Nevada.

Figs. 2, 6–9, 11, 12, 14. *Orecopia cotei* sp. nov. 2, 8, 9, 12, holotype, GSC 17633, unnamed limestone (late Frasnian), Nabesche River region, north-eastern British Columbia. 6, 11, 14, paratype 1 (before sectioning), GSC 17634, same horizon and locality as the holotype. 7, paratype 3, GSC 17636, lower part of the Tathlina Formation (middle or late Frasnian), Hay River, Northwest Territories.

Figs. 5, 10, 13. *Orecopia uchtensis* (Keyserling). Topotype? USNM 60907, Ukhta River, Timan. An early label indicates that the specimen was originally in the Museum of the Mining School at St. Petersburg and gives the age, presumably mistakenly, as Lower Devonian.



PEDDER, Upper Devonian *Orecopia*

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THE SILURIAN RUGOSE CORAL *MICROPLASMA LOVENIANUM* DYBOWSKI FROM MONMOUTHSHIRE

by D. E. WHITE

ABSTRACT. Specimens of *Microplasma lovenianum* Dybowski 1874 from the Wenlock Limestone of the Usk Inlier, Monmouthshire, are described and illustrated. This is the first record of the occurrence of *Microplasma* in Britain. The diagnosis of the genus is re-stated and a diagnosis of *M. lovenianum* is also given.

DYBOWSKI (1873, p. 340) erected the genus *Microplasma* for fasciculate rugose corals, the septa of which are represented by thorn-like projections (trabeculae). The following species, all of Silurian age, were described and figured (pp. 508–14, pl. 5, figs. 3–6):

<i>Microplasma gotlandicum</i>	from the Baltic islands of Gotland and Karlsö
<i>Microplasma lovenianum</i>	from Karlsö
<i>Microplasma schmidtii</i>	from Karlsö
<i>Microplasma pectiniseptatum</i>	from Gotland

Lang and Smith (1927, p. 478, footnote), in rejecting the views of Schlüter (1889) and Počta (1902) concerning *Cystiphyllum sihriense* Lonsdale and *C. cylindricum* Lonsdale, state that they 'recognise *Microplasma* for compound *Cystiphyllum*'.

Wedekind (1927, pp. 63–64) considered *Microplasma* to be a dwarf form of *Cystiphyllum*, in which only the central part of the internal structure is present. He selected *M. gotlandicum* as the type species. This was the first valid selection.

Prantl (1940) rejected Wedekind's views. He slightly amended Dybowski's diagnosis of *Microplasma* to include the presence of 'spinose ridges on successive dissepimental floors' as well as in the peripheral stereozone. He wrongly considered it to be congeneric with *Aphyllum* Soshkina 1937. The tabulae are complete and widely spaced in *Aphyllum*, affinities of which are closer to the family Tryplasmataidae Etheridge 1907. In the same paper, Prantl described and figured *Microplasma flexuosum* from the Upper Wenlock, eastern part of the quarry 'America', near Budňany, Bohemia. He considered this species to be 'very closely allied with *M. schmidtii*, with which it is perhaps conspecific'. Prantl suggested that *M. schmidtii* and *M. gotlandicum* 'represent only the different ontogenetical stages of growth of the same species'.

In October, 1961, during the resurvey of the One-Inch Newport (249) Sheet by the Geological Survey, Mr. J. D. D. Smith and the author visited a Wenlock Limestone quarry [National Grid Reference—ST/33989839], 550 yd. E. 13° S. of the church, Common Coed-y-Paen, Monmouthshire. Among the fossils collected were two specimens of parts of large fasciculate coral colonies, later identified as *M. lovenianum*. They are described below. A brief note on this occurrence has already been published (White 1965).

SYSTEMATIC PALAEOONTOLOGY

Family CYSTIPHYLLIDAE Milne Edwards and Haime

Genus MICROPLASMA Dybowski, emend. Prantl

Type species. M. gotlandicum Dybowski; Wedekind 1927

Diagnosis (after Prantl 1940): Rugose coral with phaceloid corallum of thin, cylindrical, scolecoïd corallites. Septa represented by trabeculae projecting internally from a narrow peripheral stereozone; also present on upper surfaces of horizontal skeletal elements. Dissepiments and tabellae not always separately recognizable.

Microplasma lovenianum Dybowski 1874

Plate 22, figs. 1–11

1874 *Microplasma lovenianum* Dybowski, pp. 510–11, pl. 5, figs. 4, 4a

Material. GSM 102583, 102583a–c, and PF 2903–4; parts of a colony from the lower part of the section; GSM 102584 and 102584a–c, parts of a colony from a loose block. Both specimens are from a small quarry, 550 yd. E. 13° S. of the church, Common Coed-y-Paen, Monmouthshire (N.G.R. ST 33989839). They are in the Geological Survey and Museum collections, London.

Diagnosis. *Microplasma* in which dissepiments and tabellae are numerous, closely spaced, irregular, and of very variable size. Peripheral increase.

Description. Corallum phaceloid. Corallites upright, scolecoïd, closely spaced, cylindrical to sub-cylindrical, with occasional deformation when in contact (Pl. 22, fig. 3). Length of protocorallites exceeds 40 mm.; maximum diameter 10 mm. Five hystero-corallites, averaging 3.5 mm. diameter, forming in calice of protocorallites, at 8.5–10 mm. diameter, by characteristic peripheral increase (Pl. 22, figs. 6, 7). Calice steep-sided, depth variable up to 9 mm. Epitheca worn, not clearly seen, thin with trace of transverse and vertical ribbing (Pl. 22, figs. 10, 11). Peripheral stereozone, thickness 0.1–0.15 mm., from which trabeculae project internally (Pl. 22, figs. 4, 5). Internal vesicular structure of small, steeply dipping dissepiments, convex upwards, and incomplete tabulae (tabellae), flat-lying, convex upwards, occasionally difficult to distinguish, with trabeculae present as small, thorn-like projections (Pl. 22, fig. 4).

Discussion: The genus *Microplasma* has not previously been recorded from Britain. The specimens from the Usk Inlier agree very closely with Dybowski's illustrations of *M. lovenianum* from the Baltic island of Karlsö, which are reproduced on Plate 22, figs. 1, 2, and with his description of the species, except that he did not mention trabeculae on the horizontal skeletal elements. However, Wedekind (1927, pl. 19, fig. 6) figured a specimen of *Microplasma* sp. with well-developed trabeculae in this position, and Prantl (1940, p. 105), in his re-definition of the genus, mentioned 'septae reduced to mere spinose ridges on successive dissepimental floors and especially on the periphery engulfed in secondary tissue'. Therefore it is considered that the presence of trabeculae on the internal vesicular tissue of the specimens from the Usk Inlier does not justify the erection of a new species.

The characteristic peripheral increase of *M. lovenianum* is well seen. In GSM 102583 (Pl. 22, fig. 6), neo-tissue has developed in two calices and the resulting five hystero-

corallites are present in each case in GSM 102583c (Pl. 22, fig. 7). This process takes place quite rapidly as the two sections are approximately 3 mm. apart. This type of increase has been fully described and illustrated by Smith and Tremberth (1929, pp. 370–2, text-fig. 2).

From *M. schmidtii*, *M. gotlandicum*, and *M. flexuosum*, the specimens from the Usk Inlier differ in having a smaller internal vesicular structure. Dybowski's remaining species, *M. pectiniseptatum*, is a form more closely related to the genus *Hedstroemophyllum* Wedekind 1927 than to *Microplasma*.

AGE OF THE GENUS *MICROPLASMA*

Species of *Microplasma* described by Dybowski (1874) were from the 'Silurformation' of Gotland and Karlsö. No horizon details were given. Wedekind (1927, p. 84) mentioned that *Microplasma* is abundant in his middle and upper divisions of the 'Mittelgotlandium' of Gotland, from the upper division of which he figured *Microplasma* sp. (pl. 19, fig. 6). *M. flexuosum* Prantl 1940 occurs in the 'Motoly Beds, $e\alpha_2$ (Upper Wenlock)', near Budňany, Bohemia. Prantl (1940, p. 108) concluded that '*Microplasma* seems to be restricted to the Silurian (Wenlock–Lower Ludlow)', but suggested the possibility of an extension of its range into the Devonian.

The specimens of *M. lovenianum* from the Usk Inlier occurred within a few feet of the top of the Wenlock Limestone, a horizon which probably corresponds closely to those of the Gotlandian and Bohemian occurrences.

Acknowledgements. I record my thanks to the following: Dr. F. W. Anderson and Mr. M. Mitchell for reading through the manuscript of the paper and help during its preparation; Dr. H. Dighton Thomas for his helpful advice; publication is by permission of the Director, Geological Survey and Museum.

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EXPLANATION OF PLATE 22

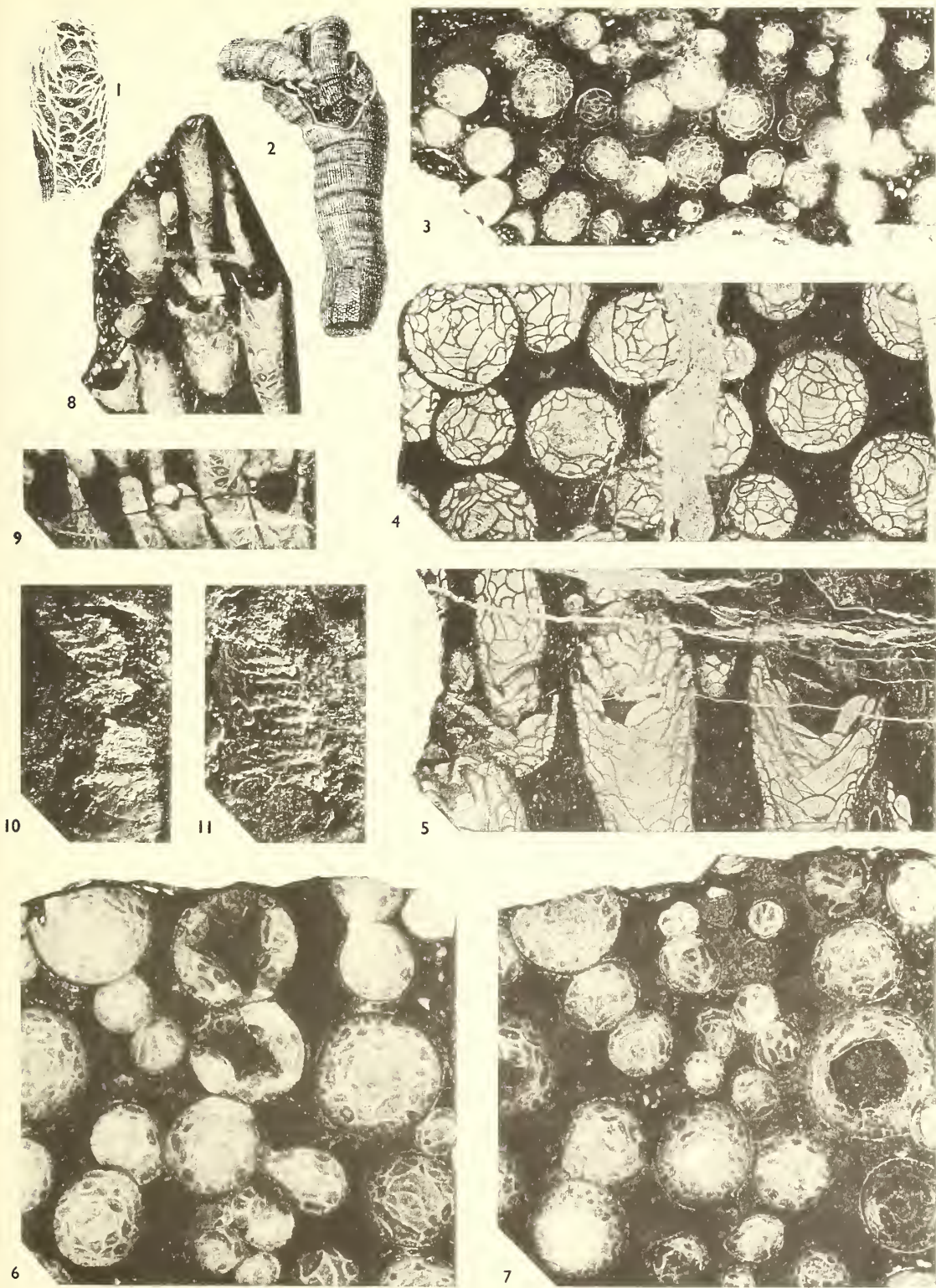
Microplasma lovenianum Dybowski 1874. Photographs by Mr. C. A. Friend, Geological Survey and Museum.

Figs. 1, 2. Reproduction of Dybowski's illustrations, 1874, pl. 5, figs. 4, 4a (fig. 4a said to be $\times \frac{1}{3}$, in error, p. 530), from 'der Silurformation' of Karlsö.

Figs. 3–8, parts of GSM 102583, from the Wenlock Limestone, Usk Inlier. 3, part of GSM 102583a. Transverse section showing deformation of corallites in contact. 4, PF 2903. Transverse section showing trabeculae on horizontal skeletal elements and projecting internally from peripheral stereozone. 5, PF 2904. Longitudinal section showing disposition of horizontal skeletal elements and trabeculae projecting from peripheral stereozone. 6, 7, part of GSM 102583 and of 102583a. Transverse sections, approximately 3 mm. apart, showing the development of neo-tissue in two calices (top middle of 6), and the resulting hystero-corallites, five from each calice (top middle of 7). 8, GSM 102583c. Longitudinal section showing hystero-corallites developing from calices of proto-corallites.

Figs. 9–11, parts of GSM 102584. Horizon and locality as for figs. 3–8. 9, GSM 102584. As for fig. 8. 10, 11, parts of GSM 102584c. Fragments of epitheca, poorly preserved; faint longitudinal ribbing and transverse wrinkles.

Figs. 1–3, 8, 9, $\times 1$, figs. 4–7, $\times 2$, figs. 10, 11, $\times 5$.



WHITE, Silurian rugose coral *Microplasma lovenianum*

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MIDDLE DEVONIAN BRACHIOPODS FROM THE ROBERTS MOUNTAINS, CENTRAL NEVADA

by J. G. JOHNSON

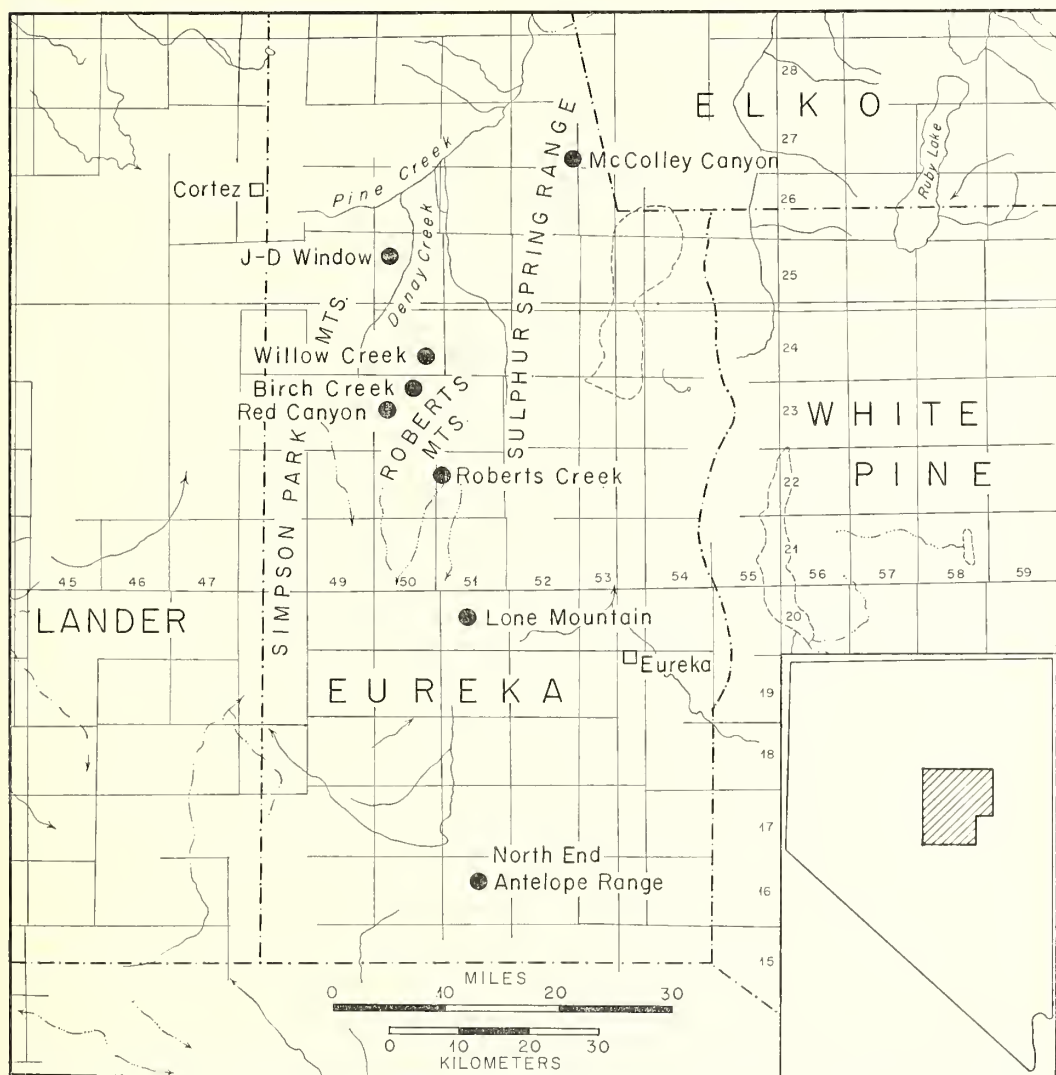
ABSTRACT. Middle Devonian stratigraphy in the Roberts Mountains is briefly reviewed and Middle Devonian limestone strata below the Devils Gate Limestone are assigned to a brachiopod-rich formation, the Denay Limestone (new name). Walcott's *Skenidium devonicum* is made type species of a new dalmanellid genus *Vallomyonia* and his *Cryptonella? circula* is assigned to *Leptathyris*. The brachiopods of the *Leptathyris circula* zone (new name) and the *Pentamerella* subzone in the lower part of the Denay Limestone are described and illustrated and their palaeontologic evidence suggests an Eifelian assignment. Fifteen species are described, fourteen from the *Leptathyris circula* zone in the Roberts Mountains. Three new species and one new subspecies are *Pentamerella wintereri*, *Hadorrhynchia eurekaensis*, *Echinocoelia denayensis*, and *Warrenella kirki praekirki*. Cyrtinacea is proposed as a superfamily.

IN 1940 C. W. Merriam published the results of his stratigraphic and palaeontologic studies of the Devonian in central Nevada (text-fig. 1). The stratigraphic column known to comprise Devonian rocks was divided into two formations, the Nevada Formation below and the Devils Gate Limestone above, and both were zoned largely on the basis of brachiopods and corals. The Nevada Formation has since been the subject of additional stratigraphic studies (Merriam and Anderson 1942; Nolan, Merriam, and Williams 1956) and the term is commonly applied to beds in Eureka County between the Lone Mountain Dolomite and the Devils Gate Limestone.

Merriam's zonal scheme (1940, p. 9) was incomplete in that he recognized the presence of an unzoned gap between the '*Spirifer*' *pinyonensis* zone and the higher *Warrenella* (= *Martinia*) *kirki* zone. Inasmuch as Merriam at that time considered the *pinyonensis* zone to be Middle Devonian, the gap appeared to be an insignificant one within the Middle Devonian.

With Merriam's work as a background, the writer in 1957 and 1958 mapped and collected fossils at significant Devonian sections in the northern Simpson Park Range. Study of the brachiopods in these collections as well as in many obtained in the Roberts Mountains by Professors E. L. Winterer and M. A. Murphy and, in addition, collections from the Sulphur Spring Range made by Carlisle, Murphy, Nelson, and Winterer (1957) led to the recognition of the new faunal zone, based on brachiopods, which filled the gap between the previously defined *pinyonensis* and *kirki* zones (Johnson 1962a). The fossiliferous beds were designated *Athyris circula* zone and *Pentamerella* subzone. The occurrence of these two brachiopod assemblages directly on beds with the *pinyonensis* zone fauna allowed a comparison for the first time and resulted in the recognition of an almost complete faunal discontinuity between the *pinyonensis* zone below and the *circula* zone above. These studies also led Johnson (1962a, p. 166) to conclude that the *pinyonensis* zone is Lower Devonian (Emsian) rather than Middle Devonian as previously thought (Merriam 1940, p. 53). The Lower Devonian assignment has since been corroborated by a restudy of the *pinyonensis* zone ammonoids (House 1962, p. 253), one of which is known to come from low in the zone. The brachiopod evidence, only touched upon earlier (Johnson 1962a, p. 166), has been thoroughly documented and discussed in

a more extensive monograph (Johnson in preparation). Studies of conodonts also indicate an Emsian assignment for the *pinyonensis* zone (Walliser in Johnson in preparation).



TEXT-FIG. 1. Eureka County and environs, central Nevada. Shaded portion of the inset map of Nevada delineates the area shown.

The faunal discontinuity recognized in the northern Simpson Park Range and in the northern Roberts Mountains through collections made by the writer at these localities proved to coincide with the lithologic break between argillaceous limestone of the *pinyonensis* zone and overlying ledge-forming outcrops of siliceous, platy, and flaggy grey limestone with the *Leptathyris circula* zone fauna. In a second paper (Johnson 1962b) the writer attempted to trace the lithologic break eastward from the fossiliferous

sections. In the limestone sections the break had already proved to be a significant one for geologic mapping and beds below it were named the McColley Canyon Member of the Nevada Limestone by Carlisle and others (1957, p. 2181). Johnson (1962*b*, p. 543) recommended that in view of coincident faunal and lithologic breaks at the top of the McColley Canyon that the surface of the discontinuity probably indicated unconformity and recommended that the McColley Canyon be elevated to formational rank.

DENAY LIMESTONE

Application of the name McColley Canyon Formation to the Lower Devonian rocks between the Lone Mountain Dolomite below and the *Leptathyris circula* zone beds at the base of the Middle Devonian section above, left unnamed Middle Devonian limestones present in the northern Simpson Park Range and in the Roberts Mountains. Neither the Sulphur Spring Range terminology of Union Mountain Sandstone and Telegraph Canyon Dolomite (Carlisle *et al.* 1957), nor Simonson Dolomite, extensively applied to Middle Devonian rocks east of Eureka County, is applicable to these sections. Neither is Nolan, Merriam, and Williams's member division of the upper Nevada, into Sentinel Mountain Dolomite, Woodpecker Limestone, and Bay State Dolomite applicable in this area on either a member or formation basis. To eliminate this deficiency the writer proposes the name Denay (Da'y-nee) Limestone as a formation composing Middle Devonian limestone strata in the northern Simpson Park Range and in the Roberts Mountains (principally northern Roberts Mountains) that together with the underlying McColley Canyon Formation constitute the Nevada Group in this area. The name comes from Denay Valley which separates the north-eastern tip of the Simpson Park Range from the north flank of the Roberts Mountains. According to Winterer (oral communication 1961) the Denay Limestone interfingers with Simonson-like dolomites in the southern Roberts Mountains. The type section of the new formation, approximately 1,000 ft. thick, is on the east flank of Willow Creek Canyon on the north side of Roberts Mountains upsection from the point where the Lone Mountain-McColley Canyon Formation contact crosses Willow Creek (elev. 6,570 ft.) due east to an elevation of approximately 7,320 ft., west of the ridge that is capped by Devils Gate Limestone east of Willow Creek. The contact between the top of the McColley Canyon Formation and the base of the Denay Limestone is met at approximately 6,840 ft. in this section. An excellent supplementary section is exposed in the J-D window of the northern Simpson Park Range between Red Hill (sec. 17, T. 25 N., R. 50 E.) where the Denay is in contact with the overlying Devils Gate Limestone, and a point about a mile to the south-west where a small section of the upper McColley Canyon Formation is present at its base. This is the same as the section of 'unnamed limestone' depicted in the column for J-D Window in an earlier paper (Johnson 1962*b*, fig. 3).

AGE AND CORRELATION

Before outlining the evidence from the brachiopods it will be useful to discuss the occurrence of a goniatite-bearing collection from the Denay Limestone in the southern Roberts Mountains that bears on the problem of the age of the *Leptathyris circula* zone. According to Winterer (oral communication 1959), who has mapped the Palaeozoic rocks

in the Roberts Mountains, the stratigraphic unit here named Denay Limestone consists of a lower well-bedded limestone member and an overlying thick-bedded limestone member in its lower half as well as one or two higher members with which we are not concerned here. So far as the writer has been able to observe personally in the field and deduce from examination of collections made by others, the *Leptathyris circula* zone includes beds that lie within the lower well-bedded unit. In 1959, Winterer made a collection (loc. 4745) in the southern Roberts Mountains about 200 ft. above the lower well-bedded unit that is rich in brachiopods, pelecypods, several types of gastropods, and in addition several specimens of the goniatite *Cabrieroceras* aff. *crispiforme* (Kayser); the latter identification being made for the writer by Dr. M. R. House (written communication 1963 and House 1965). According to House, *C. crispiforme* itself is the guide fossil to the basal Givetian zone to which it gives its name and the occurrence of specimens in the Roberts Mountains designated *C. aff. crispiforme* suggests that the containing beds be regarded as basal Givetian. Thus, according to the goniatite evidence, the *Leptathyris circula* zone lies, apparently in its entirety, below beds of earliest Givetian age and either is Eifelian or is itself very early Givetian in age.

Twenty-three species of brachiopods are recognized in the *L. circula* zone including its basal *Pentamerella* subzone and of these fourteen are described and illustrated in this paper:

Vallomyonia devonica, 'Schuchertella' sp., *Pentamerella wintereri*, *Gypidula* cf. *recurrens*, *Hadorrhynchia eurekaensis*, *Leiorhynchus* sp., *Spinatrypa* sp. B, *Vagrana*? sp., *Dubaria*? cf. *thetis*, *Leptathyris circula*, *Warrenella kirki praekirki*, *Warrenella* cf. *columbina columbina*, *Echinocoelia denayensis*, *Cyrtina* sp.

Species of *Teichertina*, *Schizophoria*, *Mesopholidostrophia*?, *Productella*, *Spinatrypa*, *Anatrypa*, *Nucleospira*, *Meristina*?, and *Quadrithyris* are represented by inadequate material. The occurrence of *Vallomyonia devonica* at present has no value for correlation since the genus is unknown outside of Nevada. 'Schuchertella' is fairly common in Lower and Middle Devonian rocks and is of no help in precise correlation. *Pentamerella wintereri* is most like species of Eifelian age in the Ural Mountains (Khodalevich 1951) and differs quite strongly from the myriad of species of the Hamilton- Traverse rocks of the eastern United States. *Gypidula* cf. *recurrens* is perhaps identical with Meyer's species which occurs in the Blue Fiord Formation of Ellesmere Island. According to McLaren (in Fortier et al. 1963, p. 61) the Blue Fiord Formation is of Eifelian age. *Hadorrhynchia* is typical of *Stringocephalus*-bearing beds in north-west Canada, but the species from the Denay Limestone is a new one. The same may be said for *Leiorhynchus* since the species apparently has not yet been reported beyond central Nevada. *Spinatrypa* sp. B is probably a new species and is quite unlike typical *Spinatrypa* species that are fairly well known in the Givetian of western Canada. Both *Vagrana* and *Dubaria* cf. *thetis* are questionably assigned and so should be given little weight in correlation. If the latter identifications could be placed on firmer ground they would probably indicate an Eifelian age for the containing beds in Nevada since they are most common in Lower Devonian and Eifelian in the Old World. *Leptathyris*, represented by *L. circula*, is a recently defined athyridid most common in the Eifelian, but present in the Lower Devonian and inasmuch as its definition is so recent its stratigraphic range is probably insufficiently known on which to base a firm correlation. *Warrenella kirki praekirki* is of little help in distinguishing Eifelian from Givetian. Similar forms are typically Middle

Devonian. *Warrenella* cf. *columbina columbina* compares very favourably with that subspecies as illustrated by Havlíček (1959, pl. 28, fig. 3) from the Acanthopyge Limestone (upper Eifelian) of central Czechoslovakia. *Echinocoelia denayensis* differs considerably from the Tully species *E. ambocoelioides* Cooper and Williams, but is fairly close to *E. incurva* Cooper and Williams, from the Mottville Member at the top of the Marcellus (or base of the Skaneateles) in New York State. According to the goniatite evidence discussed by House (1962, p. 254) at least part of the Marcellus is Givetian and *E. incurva* would be of earliest Givetian age. *E. denayensis* is also close to *E? rogeri* (= *Ambocoelia rogeri* Drot 1955, p. 565, pl. 27, fig. 3a-d) which is reported to be of late Eifelian (Couvianian) age. *Cyrtina* is common throughout the Devonian and so is of no help in precise correlation.

In summary, the brachiopods appear to have their closest relations to brachiopod species from beds elsewhere assigned to the Eifelian, possibly high Eifelian, and some lesser affinity with Givetian species. The goniatite occurrence also suggests that beds bearing the *L. circula* fauna are older than early Givetian.

There seems to be little reason to pursue the possibility that beds within the *L. circula* zone could be Lower Devonian inasmuch as the underlying 'Spirifer' *pinyonensis* zone fauna is completely different and is very high Lower Devonian, Emsian, and possibly upper Emsian (Johnson in preparation). It is suggested, therefore, that the combined evidence is sufficient to indicate a tentative Eifelian assignment for the *L. circula* zone.

The stratigraphic occurrence of the *L. circula* zone south of the area studied by the writer in the Simpson Park Range and Roberts Mountains can be deduced from data published by C. W. Merriam. Merriam (written communication 1958) indicated that forms identical to those listed as *L. circula* in this paper occur in the 'lower Nevada Formation' at the north end of the Antelope Range. Merriam (1940, p. 23; 1963, p. 45, table 2) includes some 718 ft. of strata in his 'lower Nevada' unit at Lone Mountain. However, he notes that the lower 530 ft. is much more fossiliferous than the remaining part of the 'lower Nevada'. Probably, beds between 530 and 718 ft. above the base of the Nevada at Lone Mountain belong to the *L. circula* zone and taken in conjunction with Merriam's recognition of *L. circula* in his 'lower Nevada' in the Antelope Range, indicates that the views of the writer and of Merriam are in essential harmony regarding what part of the fossiliferous western sections is equivalent to the Oxyoke Canyon Sandstone to the east. Johnson (1962b, fig. 3) has already concluded that the Union Mountain Sandstone (= Oxyoke Canyon Sandstone) is at least partially equivalent to the *L. circula* zone, an identical position as that which would be indicated by the presence of the *L. circula* zone at the top of Merriam's 'lower Nevada' (1963, p. 45, table 2).

Outside of central Nevada the only brachiopod faunas that appear to bear any resemblance to that of the *L. circula* zone are reported from north-western Canada and from the Canadian Arctic Archipelago. Few of the significant forms of the *L. circula* zone have been reported in these areas although 'Athyris' *circula* was reported from the upper Hume Formation of the MacKenzie Basin by Warren and Stelck (1962, p. 278). The species *Gypidula* cf. *recurrens* may prove to be significant for correlation in the Eifelian in western North America and in the Arctic since it is reported from the Blue Fiord Formation of Ellesmere Island. According to Dr. A. W. Norris of the Geological Survey of Canada (written communication, December 1964), the specimens referred

to here as *Gypidula* cf. *recurrens* compare most closely with a form present in the upper Blue Fiord Formation (GSC loc. 26525). Crickmay's report (1962, p. 3) of *G.* cf. *pseudogaleata* from the Bear Rock Formation (called by him Lower Devonian) may be an occurrence of a similar form. Crickmay reported the species to be present with *Fimbriospirifer*, a form present in the Blue Fiord, but not present in Lower Devonian faunas of

N. ROBERTS MOUNTAINS		EUREKA DISTRICT	
D E N A Y	<i>Warrenella</i> <i>occidentalis</i> Zone	N E V A D A F M. (UPPER PART)	Bay State Dolomite with <i>Stringocephalus</i>
	Unzoned beds with <i>Schizophoria mcfarlanei</i> <i>Stringocephalus</i> , <i>Ladjia</i> , <i>Subrensselandia</i> , " <i>Atrypa</i> " cf. <i>insquamosa</i> , & <i>Hadorrhynchia sandersoni</i>		Ls. Beds with <i>Stringocephalus</i> and " <i>Rensselandia</i> " ----- Beds with <i>Schizophoria mcfarlanei</i> & large <i>Atrypa</i>
	<i>Warrenella kirki</i> Zone		Woodpecker Beds with <i>Warrenella kirki</i> & <i>Leiorhynchus nevadensis</i> ----- Beds with small <i>W.</i> cf. <i>kirki</i> & small <i>L.</i> cf. <i>nevadensis</i>
	<i>Leptathyris circula</i> Zone & <i>Pentamerella</i> Subzone		Sentinel Mountain Dolomite ----- Oxyoke Canyon Sandstone

TEXT-FIG. 2. Suggested local correlation between the brachiopod-rich Denay Limestone on the north side of the Roberts Mountains and the sequence of mainly dolomite members of the Middle Devonian part of the Nevada Formation in the Eureka district (Nolan *et al.* 1956). '*Rensselandia*' in the Eureka district was examined on loan from Dr. C. W. Merriam after this paper went to press. Merriam's specimens are large and well preserved and upon preparation prove to belong to *Subrensselandia*.

central Nevada studied by Johnson (in preparation). More adequate comparisons of correlative faunas must await description and illustration of more of the oldest Middle Devonian species in Canada.

The stratigraphic position of the *L. circula* zone and *Pentamerella* subzone is depicted in text-fig. 2 which shows the relations of the assemblage zones and undefined faunal units of the Denay Limestone on the north side of the Roberts Mountains in comparison with the faunal sequence of the upper part of the Nevada Formation of the Eureka District as reported by Nolan, Merriam, and Williams (1956, p. 47).

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA

Suborder ORTHOIDEA

Superfamily ENTELETACEA Waagen 1884

[*nom. transl.* Alikhova 1960 (*ex* Enteletinac Waagen 1884)]

Family SCHIZOPHORIIDAE Schuchert and LeVene 1929

Genus VALLOMYONIA gen. nov.

Type species. Skenidium devonicum Walcott 1884, p. 116, pl. 13, fig. 4, 4a.

Discussion. The new genus is represented only by minute or small shells with a shallow dorsal sulcus. Internally very small pedicle valves bear minute dental lamellae, but larger specimens with the width of about a centimetre completely lack them. In the brachial valve the structures are for the most part delicate. The cardinalia consist of thin, widely divergent brachiophores to which are attached long rod-like brachiophore processes. The brachiophores of very small specimens are supported by short, thin, brachiophore supporting plates that are continuous anteriorly with ridges bounding the muscle field laterally and short, thin, fulcral plates serve as the bases of the sockets. Larger specimens, with a maximum width of about a centimetre, have more strongly differentiated muscle bounding ridges that have become separate from the brachiophore bases and lie outside of them—giving a greater relative width to the posterior adductor muscle scars. Larger specimens also show the anterior adductor scars enclosed anteriorly and the whole of the antero-lateral margin of the muscle field is slightly elevated by the well-developed muscle bounding ridges. Both minute and small specimens bear a high, triangular median septum that extends from near the base of the cardinal process to the anterior margin of the shell.

The genus *Prokopia* Havlíček 1953 was considered by the writer as a possible receptacle for Walcott's species and specimens of *Prokopia bouskai* from the Eifelian Trebotov limestones kindly sent by Dr. Vladimír Havlíček have a relatively strongly convex pedicle valve and appear to lack dental lamellae, however, the hinge teeth are relatively ponderous and are supported postero-laterally by shell material deposited in the umbonal cavities, thus short dental lamellae, if present, could have been made obsolescent. The ventral muscle field of *Prokopia* is broadly transverse and approximately semi-circular in outline, separated from the interior of the valve along its anterior edge by a small step or elevated platform similar to that developed in small specimens of *Levenea*. The median septum of *Prokopia* is very high and triangular and apparently reaches nearly to the anterior edge of the valve. Its adductor muscle field is bounded antero-laterally by relatively strongly impressed margins that define a pair of triangular muscle impressions much the shape as are present in *Hypsomyonia*, however, the anterior edges of the muscle bounding ridges are not elevated above the floor of the valve as in the latter genus. On the specimen of *Prokopia* at hand it is not possible to detect fulcral plates. The sockets apparently are defined by shell material connecting the bases of the brachiophores laterally with the floor of the valve.

Vallomyonia resembles *Monelasmia* Cooper 1955 (see also Pedder 1959) in some respects, but Cooper's genus bears strong dental lamellae in the ventral valve and a

relatively long pair of diductor muscle impressions. The cardinalia of *Monelasma*, in addition, are of the *Schizophoria* type, that is, with well-developed brachiophore supporting plates in contrast to the relatively minute ones seen only on very small specimens of *Vallomyonia*. *Vallomyonia* seems closest to Cooper's genus *Hypsomyonia* (1955) from the Frasnian Independence Shale of Iowa and so far as their differences can be evaluated the two genera can be distinguished by only slight elevation of the muscle bounding ridges in the brachial valve of *Vallomyonia* in contrast to *Hypsomyonia* in which the whole adductor muscle field is elevated above the floor of the valve. *Vallomyonia* is the most logical ancestor to *Hypsomyonia* that has come to the writer's attention.

Vallomyonia devonica (Walcott 1884)

Plate 23, figs. 1–17

Material. The holotype, USNM no. 13827, was borrowed from the U.S. National Museum. It is a silicified specimen attached to a small slab of limestone and is from the same locality of Walcott's at Lone Mountain (553) as are the types of *Leptathyris circula*. There are several other specimens of *L. circula* on the type slab.

Figured specimens. USNM nos. 145478–83, 145538, 145538A, 145538B.

Exterior. The shells are minute to small, transversely suboval to subquadrate in outline, and unequally biconvex in lateral profile. The pedicle valve is relatively low and not strongly convex and is faintly carinate. The brachial valve is nearly flat or gently convex and markedly sulcate. The interarea of the pedicle valve is steeply apsacline to nearly catacline, low, triangular, and nearly flat. The delthyrium is triangular and open, enclosing an angle of about 40°. Among the larger specimens, approaching a centimetre in maximum width, there is commonly a small concave plate inside the apex of the delthyrium. The ventral beak is short. The interarea of the brachial valve is long, flat, and anacline.

The ornament consists of numerous subangular costellae of several sizes which increase in number anteriorly by bifurcation and by implantation. The shell substance is relatively thin and delicate, and is endopunctate.

Interior of pedicle valve. The hinge teeth are small, stubby, and triangular with their long edges parallel to the interarea of the valve. They are supported basally by very short, thin, widely divergent dental lamellae which define a transverse, apically situated, ventral muscle field. Larger specimens have the dental lamellae almost completely obsolescent. The muscle field is transverse and smooth, unfaceted, and undivided medially by a myophragm. Its anterior edge is at the same level as the interior of the valve or is slightly elevated in larger specimens. The interior is crenulated in the anterior half of the shell or peripherally by the impress of the costellae.

Interior of brachial valve. The cardinal process is bilobate, short, and triangular with its myophore face approximately parallel to the plane of the interarea. It is supported basally by the posterior end of the median septum and postero-laterally by a pair of ancillary struts (Williams and Wright 1963, p. 9). The latter structures, however, join laterally to the brachiophores and not to brachiophore supports. The brachiophores are slender and suboval in cross-section and are extended as long slender brachial processes toward the

ventral valve and with a slight anterior inclination. The sockets are defined between the interarea and the brachioophores in very small shells by minute fulcral plates that are elevated well above the floor of the valve. Brachioophore supporting plates on very small specimens diverge moderately antero-laterally and recurve to become subparallel to the midline and continue as ridges bounding the lateral edges of the unpartitioned adductor muscle field. On larger specimens brachioophore supporting plates are obsolescent and the muscle-bounding ridges become more widely set apart and distinct from the brachioophore bases. Also the posterior adductors become relatively wider and the whole adductor muscle field becomes elevated along its margin. A high triangular median septum is present from the base of the cardinal process almost to the anterior edge of the valve. The interior is moderately to strongly crenulated by the impress of the costellae.

Occurrence. *Vallomyonia devonica* is a relatively common species in the *Leptathyris circula* zone in the exposures of the Denay Limestone at the north-eastern tip of the Simpson Park Range, on the north side of the Roberts Mountains at Willow Creek, and on the west side of the Roberts Mountains south of Hanson Creek and east of Red Canyon. It is also present in the *Pentamerella* subzone at Birch Creek.

Suborder PENTAMEROIDEA

Superfamily PENTAMERACEA M'Coy 1844

[*nom. transl.* Schuchert 1896 (*ex* Pentameridae M'Coy 1844)]

Family PENTAMERIDAE M'Coy 1844

Subfamily GYPIDULINAE Schuchert and LeVene 1929

Genus GYPIDULA Hall 1867

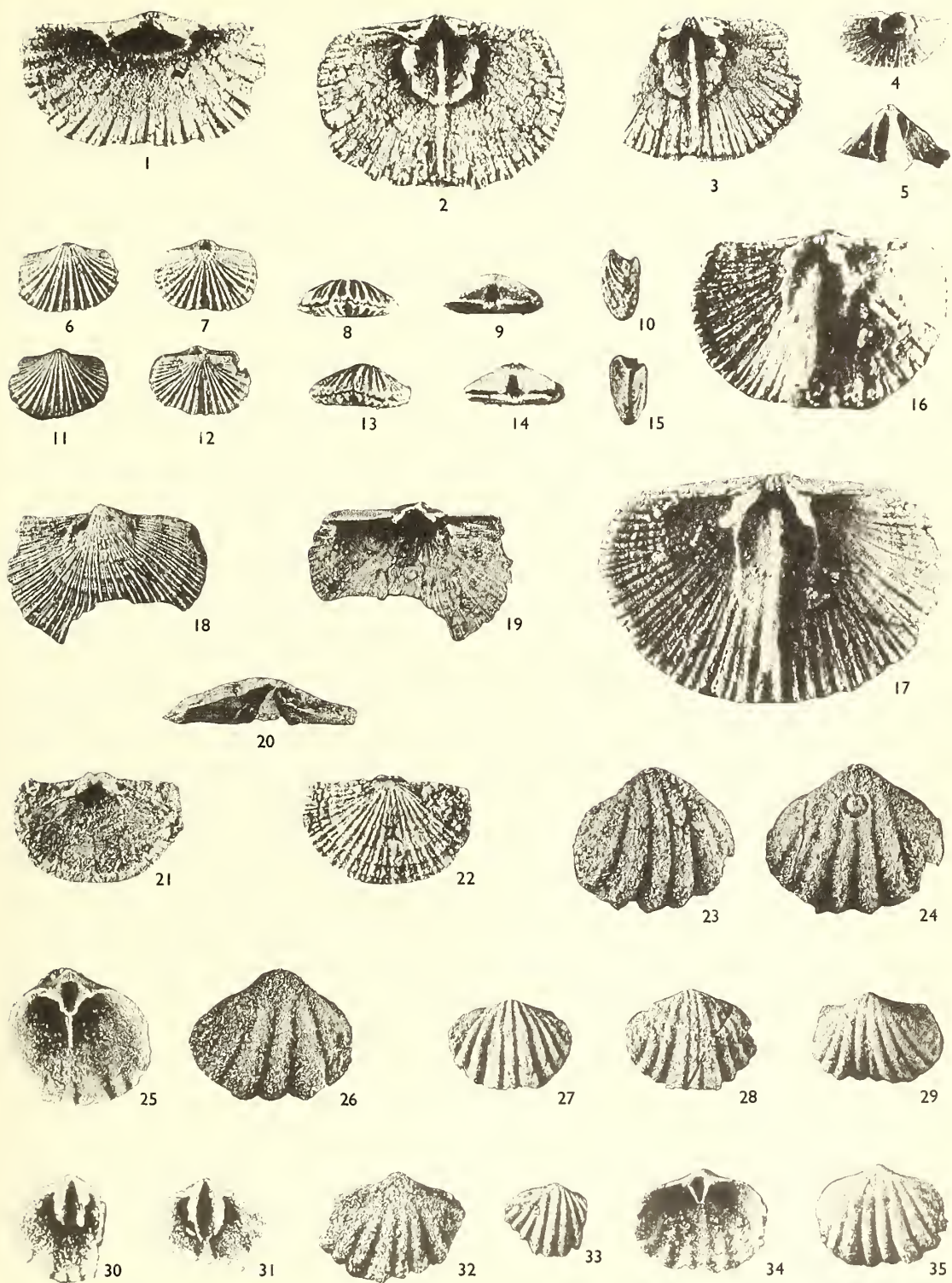
Type species. *Pentamerus comis* Owen 1852, p. 583, pl. 3A, fig. 4.

EXPLANATION OF PLATE 23

Figs. 1–17. *Vallomyonia devonica* (Walcott). 1–3, *Pentamerella* subzone, locality 4744, northern Roberts Mountains. 4–17, lower *Leptathyris circula* zone, locality 4739. 1, Interior of pedicle valve $\times 6$, USNM 145538. 2, Interior of brachial valve $\times 4$, USNM 145538b. 3, Interior of brachial valve $\times 4$, USNM 145538a. 4, Interior of pedicle valve $\times 5$, USNM 145479. Note very short dental lamellae. 5, Oblique view of interior of fragment of brachial valve $\times 4$, USNM 145480. Note high triangular median septum. 6–10, Ventral, dorsal, anterior, posterior, and side views $\times 5$, USNM 145482. 11–15, Ventral, dorsal, anterior, posterior, and side views $\times 4$, USNM 145483. 16, Interior of brachial valve $\times 8$, USNM 145478. Note high triangular median septum. 17, Interior of brachial valve $\times 8$, USNM 145481. Note long slender brachial processes.

Figs. 18–22. '*Schuchertella*' sp. 18–20, Exterior, interior, and posterior views of pedicle valve $\times 2$, USNM 145485, *Pentamerella* subzone, loc. 4744. 21, 22, Interior and exterior views of brachial valve $\times 3$, USNM 145484, upper *Leptathyris circula* zone, loc. 4737.

Figs. 23–35. *Pentamerella wintereri* Johnson sp. nov. *Pentamerella* subzone, lower *Leptathyris circula* zone, northern Roberts Mountains. 23, Exterior of pedicle valve $\times 3$, USNM 145496, loc. 4741. 24, Exterior of pedicle valve $\times 3$, USNM 145497, loc. 4741. 25, Interior of pedicle valve $\times 4$, USNM 145494, loc. 4740. 26, Exterior of pedicle valve $\times 3$, USNM 145495, loc. 4741. 27, Exterior of brachial valve $\times 2$, paratype, USNM 145488, loc. 4744. 28, Exterior of brachial valve $\times 2$, paratype, USNM 145487, loc. 4744. 29, Exterior of pedicle valve $\times 2$, holotype, USNM 145486, loc. 4744. 30, Interior of brachial valve $\times 4$, USNM 145491, loc. 4740. 31, Interior of brachial valve $\times 4$, USNM 145492, loc. 4740. 32, Exterior of brachial valve $\times 3$, USNM 145493, loc. 4741. 33, Exterior of brachial valve $\times 2$, paratype, USNM 145490, loc. 4744. 34, 35, Interior and exterior of pedicle valve $\times 3$, paratype, USNM 145489, loc. 4744.



Gypidula cf. recurrens (Meyer 1913)

Plate 24, figs. 1-7

1913 *Pentamerus pseudogaletus* Hall, mut. nov. *recurrens* Meyer p. 34, pl. 7, figs. 5A-C.*Material figured.* USNM nos. 145498-500.

Exterior. The shells are elongate subpyriform in outline and strongly unequally biconvex in lateral profile. The pedicle valve bears a relatively broad and very strongly curved umbo and the valve, along its midline, commonly curves through an arc of 180° or slightly more. The brachial valve is subquadrate in outline and is only moderately convex and cap-like. There is a low, poorly defined, elongate, narrow fold on the pedicle valve. The brachial valve bears a shallow, broad, subrectangular sulcus at its anterior and commonly projects as a short to relatively long tongue on the largest specimens. There commonly are two or three low rounded plications, strongest at the fold and sulcus near the anterior commissure, but extending along approximately the anterior two-thirds of the length of the pedicle valve. The largest specimens bear a pair of shallow furrows bordering the sulcus on the brachial valve and affecting only the posterior fourth or fifth of the length of the brachial valve. Larger specimens bear a relatively strongly developed, moderately incurved, interarea on the pedicle valve. The pedicle valve does not flare broadly toward the anterior, but maintains almost subparallel lateral extremities.

Interior of pedicle valve. There is an elongate, V-shaped, rhomboidal spondylium originating beneath the delthyrium and projecting slightly more than half its length anterior to the hinge line. It is supported along its entire length by a thin median septum, but the septum retreats slightly basally, not attaining as great a distance anterior as the distal end of the spondylium.

Interior of brachial valve. The brachial valve bears a short, flat, orthocline interarea medially that equals slightly less than half the maximum width of the valve. It consists of two long, low, flat, triangular areas with their bases at the posterior edge of the valve and the two medial basal angles meeting at the beak. The sockets are defined by the inner edges of the interarea and the postero-lateral edges of the inner plates. The inner plates are triangular in outline, diverge antero-laterally, and converge slightly basally toward the midline. The outer plates curve outward and then recurve medially in a cylindroidal fashion, then join the interior of the valve along two discrete, slightly divergent tracks.

Occurrence. The writer has collected specimens from the west flank of the Willow Creek on the north side of the Roberts Mountains and has examined several other collections made by Winterer and his students from other places in the Roberts Mountains including the southern Roberts Mountains.

Genus PENTAMERELLA Hall 1867

Type species. *Atrypa arata* Conrad 1841, p. 55.*Pentamerella wintereri* sp. nov.

Plate 23, figs. 23-35

Material. The specimen, USNM no. 145486, in fig. 29 of Plate 23 is the holotype. It is a free pedicle valve, no articulated specimens being available among several hundred studied. The holotype measures 10.8 mm. in width, 7.6 mm. in length, and 4.7 mm. in thickness. The specimens in figs. 27, 28 and 33-35 of Plate 23 are paratypes. These include USNM nos. 145587-97.

Diagnosis. Small, strongly biconvex *Pentamerella*, with strong, rounded plications.

Exterior. The shells are transversely suboval in outline and unequally biconvex in lateral profile. Pedicle valves are about twice as strongly convex as brachial valves and are very strongly incurved at the beak which, however, is short and stubby. No interarea is developed on any of the specimens examined, the palintrope curves smoothly to join the sides of the valves. The delthyrium is open and triangular. Many of the well-preserved pedicle valves bear an apical plate filling a quarter or a third of the delthyrium and covering, but not filling, the posterior end of the spondylium. The pedicle valve bears a shallow sulcus extended anteriorly as an elongate projecting tongue and the brachial valve bears a relatively well-defined median fold that accommodates the projecting anterior tongue of the pedicle valve.

The exterior bears a few strong rounded plications on each valve. Commonly there are three plications on the fold of the brachial valve and two plications in the sulcus of the pedicle valve. However, on some specimens, the pedicle valve bears a single median plication within the sulcus. On some larger specimens that bear a single medium plication in the early growth stage, a second plication may be intercalated toward the anterior. There commonly are two or three plications on each flank of the brachial valve and from two to four plications on each flank of the pedicle valve.

Interior of pedicle valve. There is an elongate spondylium of rhomboidal outline situated beneath the delthyrium and projecting anteriorly beyond the hinge line. It is supported apically by a median septum, but the length of the septum appears to be subject to some variability in its length along the base of the valve (compare figs. 25 and 34 of Pl. 23). The surface is crenulated by the impress of the plications.

Interior of brachial valve. The sockets are rudimentary, being formed by the edge of the shell on the postero-lateral edge above the inner plates. The inner plates diverge antero-laterally and converge toward the midline. The outer plates are elongate and subparallel, in some shells meeting along a line medially and in others joining the surface of the valve along a pair of discrete subparallel tracks. A number of variations may be seen between structures which are easy to classify as one type or the other. The interior is crenulated by the impress of the plications.

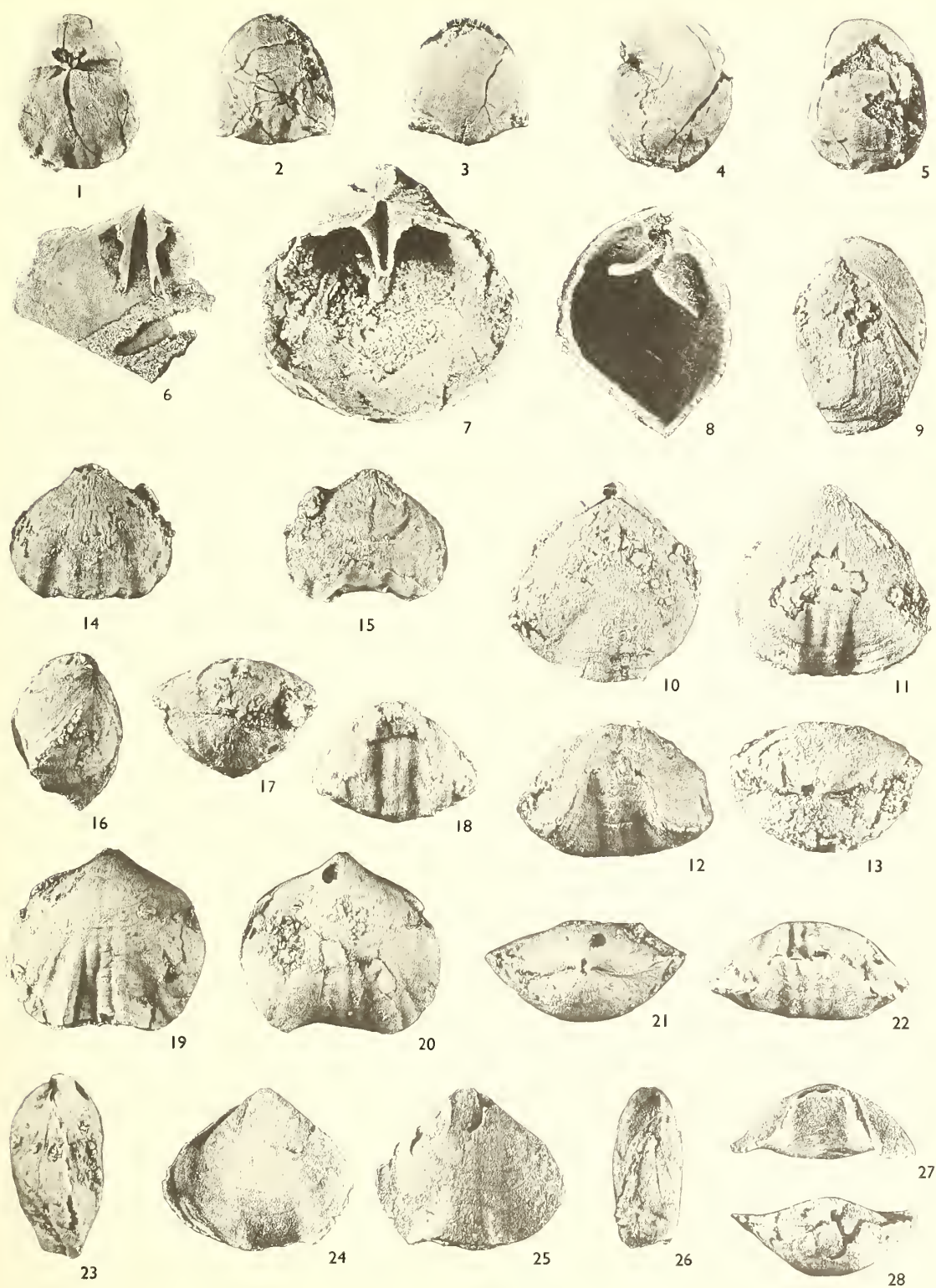
Occurrence. The new species is extremely abundant at some horizons within a few feet to 50 or 60 ft. above the base of the Denay Limestone on the north side of the Roberts Mountains. The writer has

EXPLANATION OF PLATE 24

Figs. 1-7. *Gypidula* cf. *recurrens* (Meyer). Lower *Leptathyris circula* zone, loc. 4739, northern Roberts Mountains. 1-5, Dorsal, anterior, posterior, side, and ventral views $\times 1$, USNM 145498. 6, Interior of brachial valve $\times 2$, USNM 145499. 7, Interior of pedicle valve $\times 2$, USNM 145500.

Figs. 8-23. *Leiorhynchus* sp. Lower *Leptathyris circula* zone and *Pentamerella* subzone, northern Roberts Mountains. 8, Side view of interior of both valves $\times 3$, USNM 145503, loc. 4739, lower *Leptathyris circula* zone. Note long crus, high triangular median septum, and short dental lamella. 9-13, Side, dorsal, ventral, anterior, and posterior views $\times 2$, USNM 145501, loc. 4740, *Pentamerella* subzone. 14-18, Dorsal, ventral, side, posterior, and anterior views $\times 3$, USNM 145502, loc. 4739, lower *Leptathyris circula* zone. 19-23, Dorsal, ventral, posterior, anterior, and side views $\times 2$, USNM 145504, *Leptathyris circula* zone, loc. 4743, west slope of Roberts Mountains.

Figs. 24-28. *Dubaria*? cf. *thetis* (Barrande). Lower *Leptathyris circula* zone, loc. 4739, northern Roberts Mountains. 24-28, Ventral, dorsal, side, anterior, and posterior views $\times 2$, USNM 145520.



collected slabs with abundant disarticulated specimens in both Willow Creek and Birch Creek Canyons and in the small canyon immediately east of the mouth of Willow Creek along the front of the range. Other collections have been made by E. L. Winterer in the southern Roberts Mountains in the vicinity of Roberts Creek. Cooper (1942, p. 1773) mentions the presence of small *Pentamerella* at Lone Mountain indicating that the species may be present there also. Another species of small *Pentamerella* is present in a silicified collection containing *Stringocephalus* and *Subrensselandia* in Red Canyon on the west flank of the Roberts Mountains. However, the *Stringocephalus* zone specimens bear more and finer plications. The species has not been recognized in the Denay Limestone exposures in the northern Simpson Park Range.

Comparison. The new species most closely resembles *P. suspecta* Khodalevich (1951, pl. 7, fig. 7a-d) and *P. sosvaensis* Khodalevich (1951, pl. 7, fig. 11a-d) from the Eifelian of the Ural Mountains. *P. sosvaensis* may be distinguished by being more elongate and plicate only on the anterior half of the shell. *P. suspecta* is very similar to the new species in size, relative convexity, and in the size and number of the plications. However, the illustrated specimen is somewhat more strongly rhomboidal in outline than *P. wintereri*. *P. arata* Conrad, *P. pavilionensis* Hall, and *P. dubia* Hall (Hall and Clarke 1895, pl. 71) are all much larger than the new species and thus cannot be closely compared. All appear, however, to have relatively smooth umbonal regions on both valves so that specimens the size of those typical of the Nevada fauna would be much less strongly plicate. *P. obsolescens* Hall (1867, pl. 58, figs. 24, 25) is a small species, but almost completely lacks plications. *P. thusuelda* Nettelroth (1889, p. 51, pl. 31, figs. 26-28) is a much larger and elongate species than is *wintereri*. Branson (1923) named two new species from the Middle Devonian of Missouri. *P. wintereri* contrasts strongly with one of these, *P. missouriensis*, in having a much shorter ventral beak and less prominent ventral umbo. *P. wintereri* differs from Branson's second species, *P. fultonensis*, in having plications (Branson 1923, pl. 16, figs. 21-23; pl. 24, figs. 1-4). The new species differs from *P. liorhyncha* Cooper and Cloud (1938, p. 447, pl. 54, figs. 12-16, 31-34) which is decidedly more elongate and pyriform in outline.

P. athyroides (Winchell) as illustrated by Imbrie (1959, pl. 51, figs. 6-10) is a larger species with plications not developed on the umbones. The same may be said of *P. petoskeyensis* (Imlay) and *P. papilla* Imbrie (Imbrie 1959, pl. 51, figs. 25-30, 18-24). *P. aulax* Imbrie (1959, pl. 51, figs. 11-17) has much finer plications than does *P. wintereri*. Other named species of Imbrie, *P. pericosta*, *P. lingua*, *P. aftonensis*, *P. tumida*, and *P. alpenensis* all differ from *P. wintereri* in being relatively large forms that lack plications on the umbones. *P. proteus* Imbrie (1959, pl. 53, figs. 1-8), a small species with a few plications that originate close to the posterior, differs in having a transverse subrhomboidal outline and a much smaller apical angle than do specimens of *P. wintereri*. The species *Spirifer davidsoni* Schnur (1853, pl. 35, fig. 7; pl. 44, fig. 3), a *Pentamerella* according to Havlíček (1952, p. 2, pl. 1, figs. 7, 9), is very similar to *P. wintereri* but has a considerably more prominent beak in the pedicle valve. *P. sclavus* Norris from the Middle Devonian Horn Plateau Formation of the Mackenzie District of north-west Canada (McLaren and Norris 1964, p. 37, pl. 13, figs. 9-13) is larger and has a narrower and more elongate ventral beak than does *P. wintereri*. The Canadian species *Pentamerus borealis* Meek was assigned to *Pentamerella* by Schuchert (1897, p. 302), but it appears that exception should be taken to the assignment since '*P.*' *borealis* bears a ventral fold and dorsal sulcus (Meek 1868, pl. 13, fig. 11a, b, d). In any event '*P.*' *borealis* bears little similarity to *Pentamerella wintereri*.

Suborder STROPHOMENOIDEA

Superfamily ORTHOTETACEA Waagen 1884

[*nom. transl.* Williams 1953 (*ex* Orthotetinae Waagen 1884)]

Family SCHUCHERTELLIDAE Williams 1953

[*nom. transl.* Stehli 1954 (*ex* Schuchertellinae Williams 1953)]

Subfamily SCHUCHERTELLINAE Williams 1953

Genus SCHUCHERTELLA Girty 1904

Type species. *Streptorhynchus lens* White 1862, p. 28.

‘*Schuchertella*’ sp.

Plate 23, figs. 18–22

Material figured. USNM nos. 145484–5.

Discussion. Assignment to *Schuchertella* is not firm since pseudopunctae were not observed.

Exterior. The species is small, averaging about a centimetre in width and is transversely subsemicircular to shield-shaped in outline. The valves are unequally biconvex in lateral profile with the pedicle valve more strongly convex than the brachial valve and commonly somewhat elevated with a moderately twisted beak. The ventral interarea is apsacline, flat, and triangular. Its height varies and the delthyrium is covered by a gently convex pseudodeltidium. The ornament consists of fine, rounded, slightly parvicostellae costellae that increase in number anteriorly, principally by intercalation. The costellae are crossed by a few irregularly spaced growth lines. A shallow sulcus may be developed on the brachial valve. The maximum width of the valves is attained near midlength.

Interior of pedicle valve. The hinge teeth are relatively large and triangular in horizontal section. They leave stout tracks on the inner edges of the delthyrium, but there are no supporting dental lamellae. The interior of the valve is not crenulated by the impress of the costellae.

Interior of brachial valve. The socket ridges are widely divergent antero-laterally and are unsupported on their divergent inner edges. Two short prongs of shell material are attached to the posteromedial edges of the socket ridges and project posteriorly. It was not determined whether a chilidium was present or not. The interior is not crenulated by the impress of the costellae.

Occurrence. This small species of ‘*Schuchertella*’ is present in one collection from high in the *Leptothyris circula* zone in the southern Roberts Mountains and from the *Pentamerella* subzone on Birch Creek in the northern Roberts Mountains.

Suborder RHYNCHONELLOIDEA

Superfamily RHYNCHONELLACEA Gray 1848

[*nom. transl.* Schuchert 1896 (*ex* Rhynchonellidae Gray 1848)]

Family TRIGONIPHYNCHIIDAE Schmidt 1965

Genus HADRORHYNCHIA McLaren 1961

Type species. *Pugnoides sandersoni* Warren 1944, p. 115, pl. 2, figs. 5, 6.

Hadorrhynchia eurekaensis sp. nov.

Plate 25, figs. 1–23

Material. The specimen in figs. 6–10 of Plate 25, USNM no. 145511, is designated the holotype. It measures 10·8 mm. in width, 9·8 mm. in length, and 8·0 mm. in thickness. The other illustrated specimens are paratypes. They include USNM nos. 145505–10.

Diagnosis. Multicostate *Hadorrhynchia*, costae relatively strong on the umbonal regions. Shape lenticular to subcuboidal, not reflexed.

Exterior. Most of the available specimens of this species are small or medium sized and bear a pyriform to subpentagonal outline. Commonly, smaller specimens are somewhat elongate and pyriform while the large ones develop slight irregularities in the shape resulting in the subpentagonal outline. The valves are strongly biconvex in lateral profile with the brachial valve about a quarter to a third more strongly convex than the pedicle valve. Smaller specimens are more commonly somewhat lenticular, but a lesser number of even very small specimens attain the subcuboidal outline more common to medium-sized specimens. The beak of the pedicle valve is moderately incurved and projects somewhat strongly anterior to the umbo of the brachial valve. There is a triangular delthyrium and low, apsacline, incurved interarea. The beak angle is commonly between 90° and 100° and is relatively constant for a distance equal to about a third of the length of small shells and a fourth or fifth of the length of larger shells and then decreases anteriorly to the place of maximum width which is anterior to midlength. On most specimens the pedicle valve has a relatively flattened outline along the lateral flanks as viewed from the side, then curves abruptly in a nearly geniculate fashion at the anterior commissure. The sulcus, however, attains a more uniform curvature from the beak to the anterior commissure. The pedicle valve bears a shallow median sulcus that originates in the posterior portion of the valve and becomes relatively well marked anteriorly where it is accentuated by the development of a tongue-like projection that is accommodated by a subrectangular fold in the anterior portion of the brachial valve. The ornament consists of numerous subangular costae which have smoothly rounded crests. The costae expand in size anteriorly and do not bifurcate. Commonly, the median costae on the brachial valve become relatively broad anteriorly and appear notably broader than the adjoining lateral costae at the same distance from the beak which continue strongly curving adjacent to the projecting tongue of the sulcus. Most commonly there are three costae in the ventral sulcus and four costae on the dorsal fold, but specimens with lesser and greater numbers are also encountered.

Interior of pedicle valve. The hinge teeth are small and delicate. They are supported basally by thin dental lamellae of triangular outline which are situated relatively close to the postero-lateral walls of the valve. The interior is crenulated by the impress of the costellae.

Interior of brachial valve. The sockets are long and narrow and are cylindroidal in shape, being defined postero-laterally by the inner edge of the shell and basely and ventrally by the curved hinge plates. A pair of triangular horizontal plates connects the inner edges of the outer hinge plates with the crura which arise medially on either side of a narrow V-shaped septalium that is supported by a long high median septum. The crura

are T-shaped in cross-section and curve strongly ventrally, recurving with their convex edges facing antero-laterally. The interior is fairly strongly crenulated over much of the length of the valve by the costellae.

Occurrence. This species is the most common rhynchonellid in the *Leptathyris circula* zone on the north and south sides of the Roberts Mountains. The species is also present in the *Warrenella kirki* zone overlying the *L. circula* zone in the J-D window of the northern Simpson Park Range. It appears that *Rhynchonella transversa* of Meyer (1913, pl. 7, fig. 7a-e; not Hall) from the Blue Fiord Formation of Ellesmere Island could belong to *H. eurekaensis*. Unfortunately the Arctic species is unknown internally.

Comparison. *H. sandersoni* (Warren) has much more poorly developed costae on the posterior portion of the valve. In addition, the anterior sulcus appears to be deeper on *sandersoni* and the shells are commonly relatively more transverse. Furthermore, maximum width of *H. eurekaensis* appears on almost all the shells to be developed at a somewhat greater distance anterior to the beak (McLaren 1962, pl. 7). *H. eurekaensis* appears to be distinguishable from *H. intermissa* and *H. vallorum* Crickmay (1963, pl. 7) on the same grounds that it may be distinguished from *sandersoni*.

Family LEIORHYNCHIDAE Stainbrook 1945

[*nom. transl.* Crickmay 1952 (*ex* Leiorhynchinae Stainbrook 1945)]

Genus LEIORHYNCHUS Hall 1860

Type species. *Orthis quadricostata* Vanuxem 1842, p. 168, fig. 2.

Leiorhynchus sp.

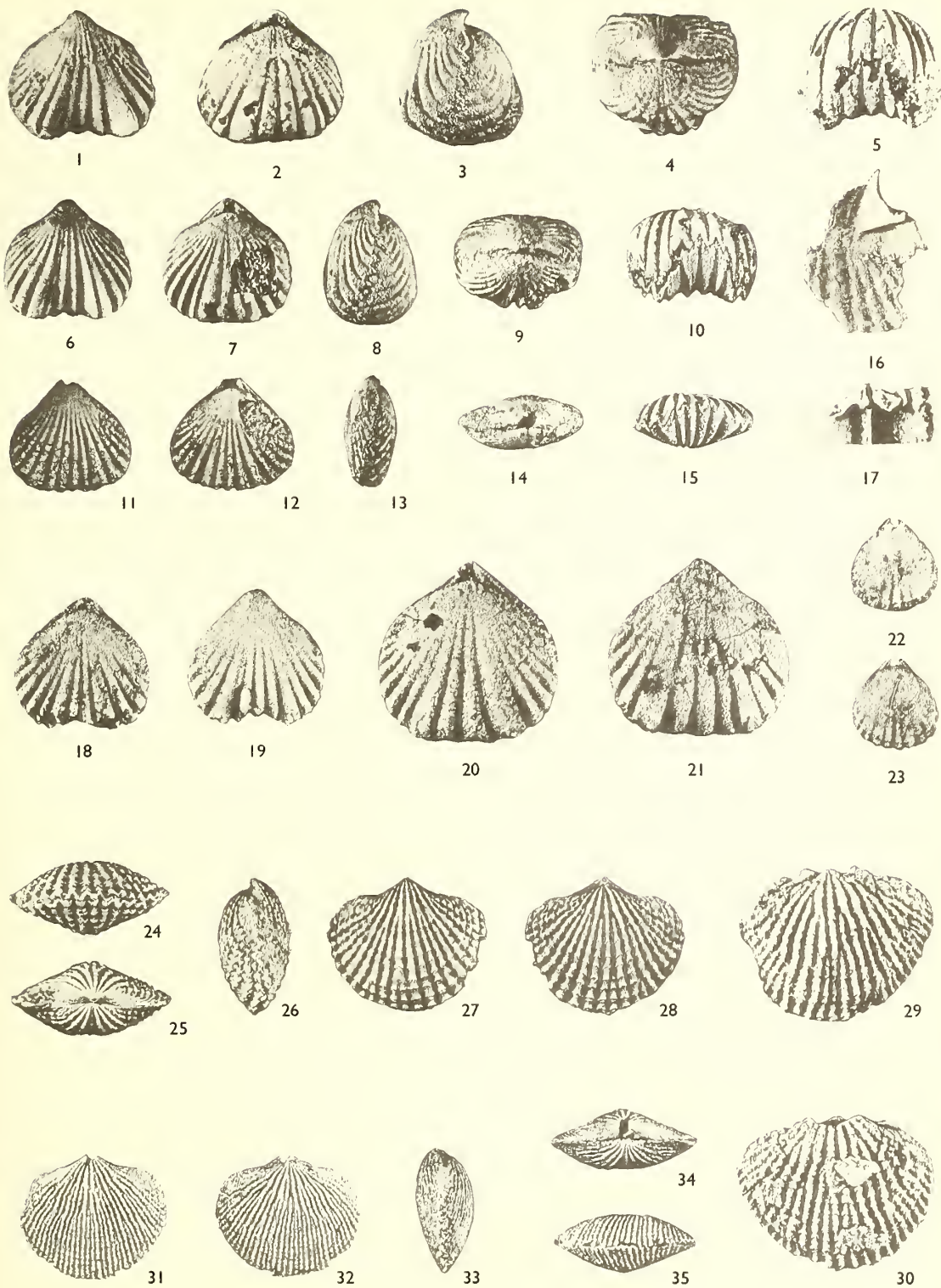
Plate 24, figs. 8-23, text-fig. 3

Material figured. USNM nos. 145502-4, 145521.

Exterior. The shells are variable in outline and convexity, commonly subpyriform to somewhat pentagonal in outline. Most specimens are strongly biconvex with the brachial valve more convex than the pedicle valve. A few specimens are relatively lenticular. The beak angle is about 90° or a little more and the postero-lateral margins are relatively

EXPLANATION OF PLATE 25

- Figs. 1-23. *Hadorhynchia eurekaensis* Johnson sp. nov. Lower *Leptathyris circula* zone, loc. 4739, northern Roberts Mountains. 1-5, Ventral, dorsal, side, posterior, and anterior views $\times 2$, paratype, USNM 145509. 6-10, Ventral, dorsal, side, posterior, and anterior views $\times 2$, holotype, USNM 145511. 11-15, Ventral, dorsal, side, posterior, and anterior views $\times 3$, paratype, USNM 145510. 16, 17, Interior of fragment of pedicle valve and posterior of brachial valve $\times 4$, paratype, USNM 145505. The two valves belong to the same individual. In fig. 16 note shape of the dental lamella. 18, 19, Dorsal and ventral views $\times 3$, paratype, USNM 145506. 20, 21, Dorsal and ventral views $\times 3$, paratype, USNM 145508. 22, 23, Ventral and dorsal views of small specimen $\times 3$, paratype, USNM 145507.
- Figs. 24-28. *Spinatrypa* aff. *lata* (Warren 1944). Near base of Telegraph Canyon Member of Nevada Formation, loc. 3536, Union Mountain, Sulphur Spring Range. Horizon probably should be assigned to *Warrenella kirki* zone. 24-28, Anterior, posterior, side, ventral, and dorsal views $\times 2$, USNM 145514.
- Figs. 29-35. *Spinatrypa* sp. B. 29, 30, Dorsal and ventral views $\times 3$, USNM 145512, loc. 4738, *Pentamerella* subzone, southern Roberts Mountains. 31-35, Ventral, dorsal, side, posterior, and anterior views $\times 2$, USNM 145513, loc. 4741, *Pentamerella* subzone, northern Roberts Mountains.



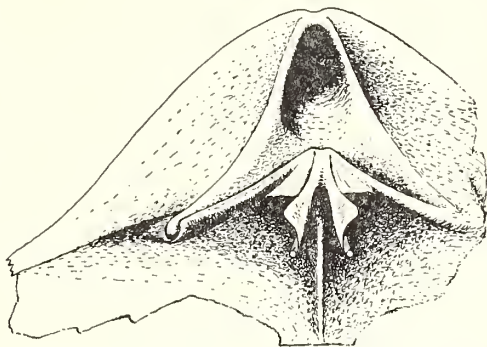
straight in the posterior third of the shell. Maximum width is commonly anterior to mid-length. The beak of the pedicle valve is strongly incurved and bears a small apical foramen. The pedicle valve bears a broad flat-bottomed sulcus in its anterior half and the brachial valve bears a corresponding subrectangular fold. In most specimens, the fold is divided medially by a shallow narrow furrow and anteriorly may bear two to four low rounded plications. Most larger specimens bear a few very short plications adjoining the fold and sulcus, but affect only a small portion of the length of the shell.

Interior of pedicle valve. The hinge teeth are small and delicate and are attached along the inner edge of the postero-lateral shell margin. They are supported by a pair of short thin dental lamellae that converge medially to join, forming a sessile spondylium. No median septum is present. The dental lamellae converge at an angle of about $75-80^\circ$.

Interior of brachial valve. The dental sockets are exceedingly narrow and diverge antero-laterally, nearly parallel to the valve margin. The crura originate at the beak and diverge at a very small angle as they project antero-

ventrally. They are circular in cross-section with fluted lateral flanges that are roughly parallel to the plane of commissure along their posterior portions, but which become depressed below the level of the crura and extend anteriorly along planes nearly parallel to the median plane (text-fig. 3). Anteriorly the bases of the crura and their lateral flanges are connected to the inner edges of the hinge plates by a pair of thin, narrow, triangular plates. Medially the dorsal edges of the crura are attached to a high median septum. No septalium is present. The median septum is long and blade-like, reaching about half way or slightly less to the anterior of the shell.

Occurrence. *Leiorhynchus* sp. is a relatively uncommon species in the *Leptathyris circula* zone on the north side of the Roberts Mountains. A number of specimens have also been collected from the Denay Limestone in the northern Simpson Park Range.



TEXT-FIG. 3. Interior of posterior portion of articulated shell of *Leiorhynchus* sp., USNM 145521. Sketch of articulating apparatus on the right side is generalized because of poor preservation. Note circular cross-section of the crura and the prominent flanges that extend ventrally from them.

Suborder ATRYOIDEA

Superfamily ATRYPACEA Gill 1871

[*nom. transl.* Schuchert and LeVene 1929 (*ex* Atrypidae Gill 1871)]

Family ATRYPIDAE Gill 1871

Subfamily ATRYPINAE Gill 1871

Genus SPINATRYPA Stainbrook 1951

Type species. *Atrypa hystrix* var. *occidentalis* Hall 1858 (*errore pro* *A. aspera* var. *occidentalis* Hall 1858, p. 515).

Spinatrypa aff. *lata* (Warren 1944)

Plate 25, fig. 24-28

1944 *Atrypa borealis* var. *lata* Warren, p. 122, pl. 3, figs. 7-9.1962 *Spinatrypa lata* McLaren and Norris, pl. 8, figs. 25-27.*Material figured.* USNM no. 145514.

Exterior. The shells are transversely suboval to subpentagonal in outline and subequally biconvex in lateral profile. The valves are more or less lenticular and none are strongly convex. A few of the smaller specimens are elongate with the maximum width near midlength or posterior to it, however, the relatively larger specimens are all transverse and have their maximum width posterior to midlength at a distance approximately one-third of the distance from the ventral beak. The ventral beak is small, pointed, and nearly straight and is pierced apically by a small circular foramen. The foramen joins anteriorly and dorsally with a broad, low, triangular delthyrium enclosing an angle greater than 90°, which is completely covered by deltidial plates that lie adjacent to the umbo of the brachial valve that has its beak incurved beneath them. On most specimens the brachial valves are of relatively even convexity across the midline, but pedicle valves are mildly carinate, except anteriorly where a faint ventral sulcus appears or is suggested by dorsal deflection of the anterior commissure.

The ornament consists of numerous, well-developed, rounded costae that increase in number most commonly by bifurcation on the pedicle valve and by intercalation on the brachial valve. They are crossed by numerous well-developed concentric growth lamellae that occur at regular intervals from the posterior to the anterior margin of the valves. The number and size of the radial costellae is variable, but in general the costae are relatively fine for the genus.

Occurrence. This species comes from just above the Union Mountain Sandstone in the northern part of the Sulphur Spring Range in beds that were incorrectly assigned to the *Heliolites* horizon by Carlisle and others (1957, loc. 3536). Present in the same collection are numerous small ambocoeliids and some small athyroids close to *Leptathyris circula*. Species of this type from the Sulphur Spring Range are regarded as a possible link between finely costellate *Spinatrypa* of the *L. circula* zone in the Roberts Mountains as well as in the northern Simpson Park Range and with *Spinatrypa* cf. *andersonensis* which is common in the typical *Warrenella kirki* zone.

Spinatrypa sp. *B*

Plate 25, figs. 29-35

Diagnosis. Transverse lenticular *Spinatrypa* with fine costellae and growth lamellae.

Material figured. USNM nos. 145512, 145513.

Discussion. This species has a size, outline, and convexity similar to *Spinatrypa* cf. *lata* described above, however, it may be distinguished by its finer ornament. The radial costellae are exceptionally fine for the genus and appear commonly to be somewhat irregular and subject to numerous bifurcations and intercalations posteriorly. Costellae remain essentially fine and narrow anteriorly. In some cases their width is less than some

of the main costellae posteriorly. They are crossed by numerous, very fine, imbricating, concentric growth lamellae.

This appears to be a new species insofar as the writer has been able to find no closely comparable form in the literature. However, the specimens available are relatively few in number and are not exceptionally well preserved. Thus, pending a more extensive collection of more adequately preserved specimens, this form will be referred to as *Spinatrypa* sp. B. This is *Spinatrypa* sp. B of Johnson (1962a, p. 166).

Occurrence. *Spinatrypa* sp. B is a common atrypoid of the *Leptathyris circula* zone and *Pentamerella* subzone in the northern Roberts Mountains and in the *L. circula* zone in the northern Simpson Park Range.

Subfamily CARINATININAE Rzhonsnitskaya 1960

Genus VAGRANIA Alekseeva 1959

Type species. *Atrypa kolymensis* Nalivkin 1936, p. 17, pl. 2, fig. 8.

Vagrana? sp.

Plate 26, figs. 1–12

Material figured. USNM nos. 145515–19.

Discussion. *Vagrana* is a strongly costate or plicate atrypoid that lacks concentric growth lamellae. Instead, as shown by Alekseeva (1960, pl. 10, fig. 3), the genus bears a fine ornament consisting of numerous, very fine pustules scattered over the surface in a quincunx pattern. Internally, large specimens carry diagnostic and unusual structures (Boucot, Johnson, and Staton 1964, pl. 128, figs. 10–12).

The specimens described below from central Nevada are very small and do not develop the structures which are known to be present in larger specimens of the genus, however, as yet we have no knowledge of the development of these same structures in small specimens of the Russian types. The exterior of the specimens, in addition, is a bit too roughly preserved to ascertain the original presence or absence of the peculiar fine ornament of the genus. In the absence of these features questionable assignment is made on the basis of the coarse ribbing and lack of concentric ornament on the specimens from the Roberts Mountains.

Exterior. The shells are elongate suboval to somewhat pyriform or subtrigonal in outline and subequally biconvex in lateral profile. The beak of the pedicle valve is short and pointed and projects posteriorly, straight or nearly straight. The hinge line is short and strongly curved and the pedicle valve bears a relatively flat palintrope consisting of two triangular flat surfaces on either side of the circular or suboval foramen present antero-dorsally to the beak of the pedicle valve. The anterior commissure is rectimarginate.

The ornament consists of well-defined, rounded, radial costae that increase in number anteriorly by bifurcation and by implantation; the latter most commonly on the brachial valve and the former on the pedicle valve (see figs. 5 and 6 of Pl. 26).

Interior of pedicle valve. The hinge teeth are thin and plate-like and are approximately perpendicular to the median line. They are attached directly to the inner edges of the valve and are not supported by dental lamellae. The interior is moderately strongly crenulated by the impress of the costae.

Interior of brachial valve. The sockets are relatively narrow and broadly divergent antero-laterally. They bear a pair of crural lobes on their inner edges. The inner edges of the crural lobes border the notothyrial cavity and diverge antero-laterally.

Occurrence. This small species of *Vagrana*? sp. is relatively common in the *Pentamerella* subzone on the north side of the Roberts Mountains at Willow Creek and in the small canyon immediately east of Willow Creek along the north face of the Roberts Mountains. The species is also present with *Pentamerella* in the southern Roberts Mountains east of Roberts Creek.

Family LISSATRYPIDAE Twenhofel 1914

[*nom. transl.* Boucot, Johnson, and Staton 1964 (*ex* Lissatrypinae Twenhofel 1914)]

Subfamily SEPTATRYPIDAE Kozłowski 1929

Genus DUBARIA Termier 1936

Type species. *D. lautenoi*s Termier 1936, p. 1266, pl. 17, 17 bis.

Dubaria? cf. *thetis* (Barrande 1847)

Plate 24, figs. 24-28

1847 *Terebratula thetis* Barrande, p. 349, pl. 14, fig. 5.

1879 *Atrypa thetis* Barrande, p. 54, pl. 86, case IV, figs. 1-11.

1951 *Septatrypa*(?) *thetis* Khodalevich, p. 84, pl. 21, figs. 6a-d.

1962 *Rhynchatrypa thetis* Siehl, p. 200, pl. 28, figs. 1, 2; pl. 37, fig. 11; pl. 38, figs. 1, 2.

Material figured. USNM no. 145520.

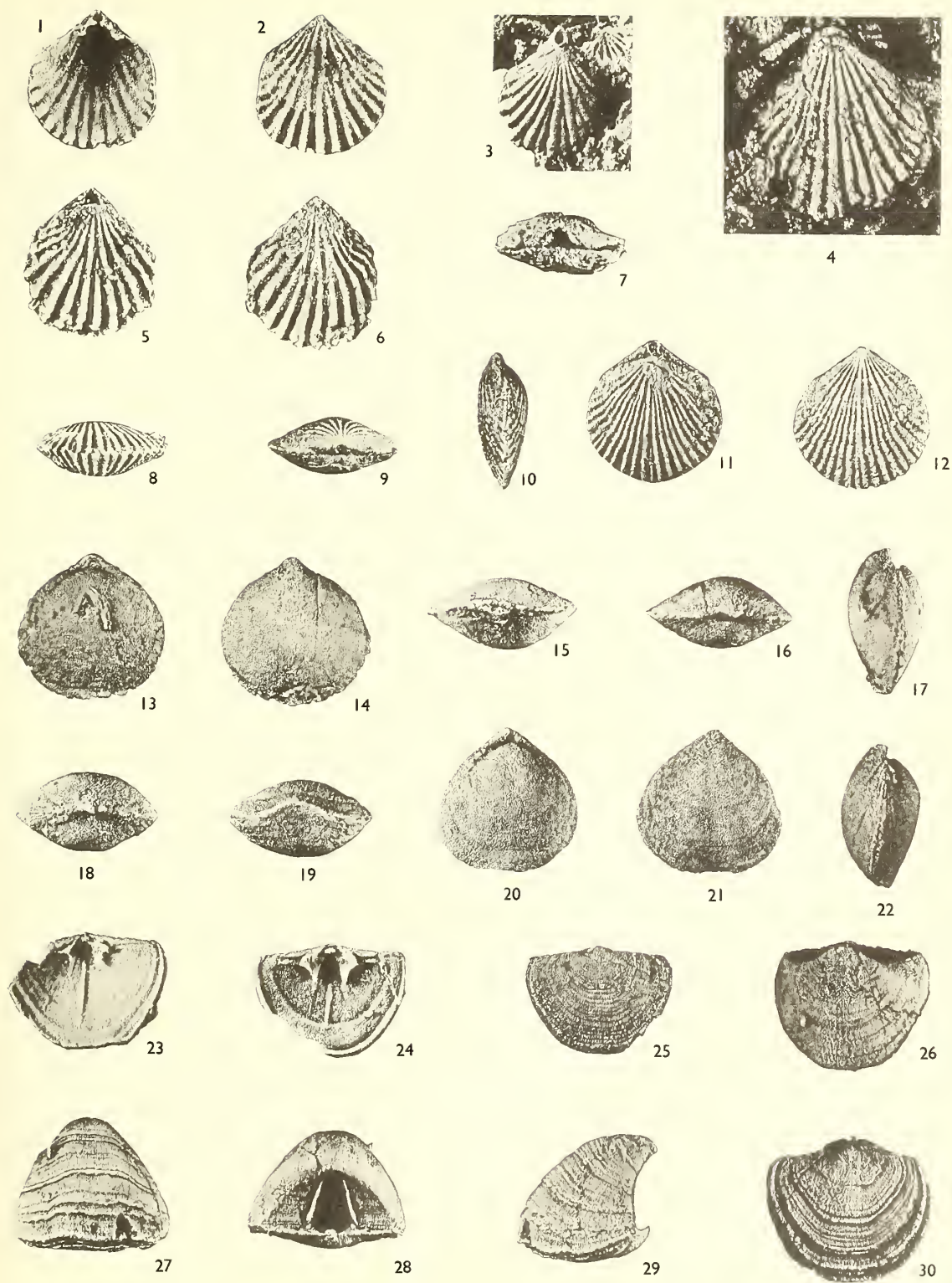
Exterior. The shell is subtrigonal in outline and lenticular in lateral profile with the pedicle valve nearly flat or reflexed and the brachial valve moderately convex. In the pedicle valve, approximately the first centimetre of shell is low convex, but antero-laterally the flanks flatten out on larger shells and the median portion becomes deflected into a deep flat-bottomed sulcus. The brachial valve is evenly rounded from the umbo to the antero-lateral flanks, but the median section is only faintly curved, nearly flat, due to the elevation anteriorly of a well-developed, rounded to nearly flat fold. The hinge line is short and moderately curved.

EXPLANATION OF PLATE 26

Figs. 1-12. *Vagrana*? sp. *Pentamerella* subzone; figs. 1-4, 8-12 northern Roberts Mountains; figs. 5-7 southern Roberts Mountains. 1, 2, Interior and exterior of pedicle valve $\times 3$, USNM 145516, loc. 4740. 3, Dorsal view $\times 3$, USNM 145518, loc. 4740. 4, Ventral view $\times 3$, USNM 145519, loc. 4740. 5-7, Dorsal, ventral, and posterior views $\times 3$, USNM 145517, loc. 4738. 8-12, Anterior, posterior, side, dorsal, and ventral views $\times 2$, USNM 145515, loc. 4741.

Figs. 13-22. *Leptathyris circula* (Walcott 1884). Lower *Leptathyris circula* zone, loc. 4739, northern Roberts Mountains. 13-17, Dorsal, ventral, anterior, posterior, and side views $\times 2$, USNM 145522. 18-22, Posterior, anterior, dorsal, ventral, and side views $\times 2$, USNM 145523.

Figs. 23-30. *Echinocoelia denayensis* Johnson sp. nov. 23, Interior of brachial valve $\times 3$, USNM 145524, loc. 4743, *Leptathyris circula* zone, west slope of Roberts Mountains. 24, Interior of brachial valve $\times 3$, paratype, USNM 145525, loc. 4739, lower *Leptathyris circula* zone, northern Roberts Mountains. 25, Exterior of brachial valve $\times 3$, paratype, USNM 145526, loc. 4739, lower *Leptathyris circula* zone, northern Roberts Mountains. 26-30, Ventral, anterior, posterior, side, and dorsal views $\times 3$, holotype, USNM 145527, loc. 4739, lower *Leptathyris circula* zone, northern Roberts Mountains.



The ornament consists of a few poorly defined concentric growth lines developed in the anterior two-thirds of the valves. No radial ornament is present.

Discussion. Unfortunately, only two specimens of this form are available and neither show the internal structures, however, the external form and lack of radial ornament are so distinctive it appears that these shells merit a provisional assignment to *Dubaria* and particularly to the broad lenticular form *Dubaria thetis*. So far as the writer knows, this form is restricted to the Emsian and Eifelian in central Europe and in the Ural Mountains, however, the genus is most common in latest Silurian and early Devonian rocks in Bohemia, the Carnic Alps, and in European and Central Asian Russia.

Occurrence. *Dubaria?* cf. *thetis* is present in a single collection in the northern Roberts Mountains on the west flank of Willow Creek in the lower *Leptathyris circula* zone.

Suborder ATHYRIDOIDEA

Superfamily ATHYRIDACEA M'Coy 1844

[*nom. transl.* Williams 1956 (*ex* Athyridae M'Coy 1844)]

Family ATHYRIDIDAE M'Coy 1844

Subfamily ATHYRIDINAE M'Coy 1844

[*nom. transl.* Waagen 1883 (*ex* Athyridae M'Coy, 1844)]

Genus LEPTATHYRIS Siehl 1962

Type species. *L. gryphis* Siehl 1962, p. 212, pl. 36, fig. 1, pl. 39, figs. 2, 3.

Leptathyris circula (Walcott 1884)

Plate 26, figs. 13–22; text-fig. 4

1884 *Cryptonella?* *circula* Walcott n. sp., p. 163, pl. 15, figs. 2, *a*, *b*.

1940 ?*Cryptonella circula* Merriam, pl. 11, fig. 8.

1962 *Athyris circula* Johnson 1962*a*, p. 166.

Material. The holotype, USNM no. 13861, was borrowed from the U.S. National Museum and was accompanied by twenty-four paratypes. They are small silicified shells with the valves tightly welded together. However, one of the paratypes has the ventral beak broken away revealing the cardinalia in the brachial valve. They exactly duplicate the structure described above from specimens collected by the writer from the Roberts Mountains. The structure of this paratype is shown in text-fig. 4. The label with the types indicates that they are from the 'Lower Devonian' at Lone Mountain.

Figured specimens. USNM nos. 145522, 145523.

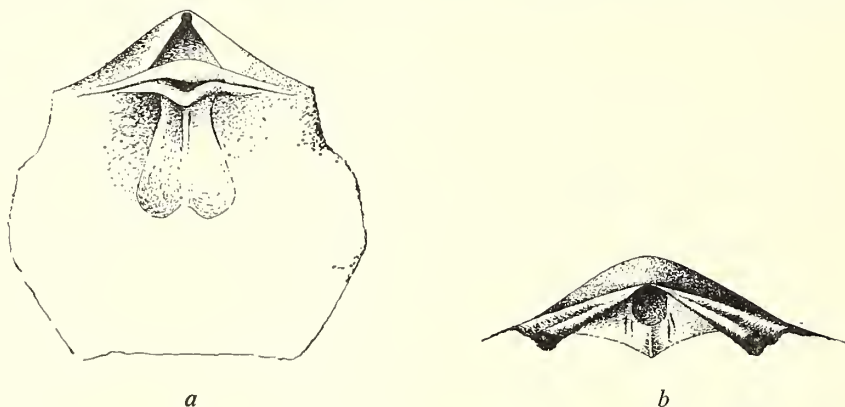
Discussion. Siehl (1962, p. 212) proposed *Leptathyris* for small non-lamellose athyridids with a thin, depressed, medially-crested, cardinal plate. These are diagnostic features of '*Athyris*' *circula*, which is therefore assigned to *Leptathyris*.

Exterior. The species is small and subcircular to elongate suboval or short pyriform in outline. In lateral profile the valves are unequally biconvex with the pedicle valve slightly more convex than the brachial valve. The ventral beak is sub-erect. The palintrope is only faintly rounded, nearly flat, but beak ridges are absent. The hinge line is short and curved. There is a triangular delthyrium commonly enclosing about 70°. It is unmodified by deltidial plates and in all the specimens examined there invariably is a minute ragged opening at the apex of the delthyrium. Its ubiquitous presence suggests that it is in fact

a mesothyrid or permesothyrid foramen. Both valves curve evenly anteriorly and anterolaterally with slightly more gentle curvature than at the umbos. There is no fold, but some specimens develop a flattened area on the anteromedial part of the pedicle valve or a faintly indented sulcus and the anterior commissure is gently deflected toward the brachial valve.

The ornament consists of a few widely spaced, faint, concentric growth lamellae. No radial ornament was observed.

Interior of pedicle valve. The hinge teeth are supported by a pair of thin dental lamellae that are situated close to the inner postero-lateral walls of the valve. The anterior edges of the dental lamellae converge slightly towards the midline and are continued for a short

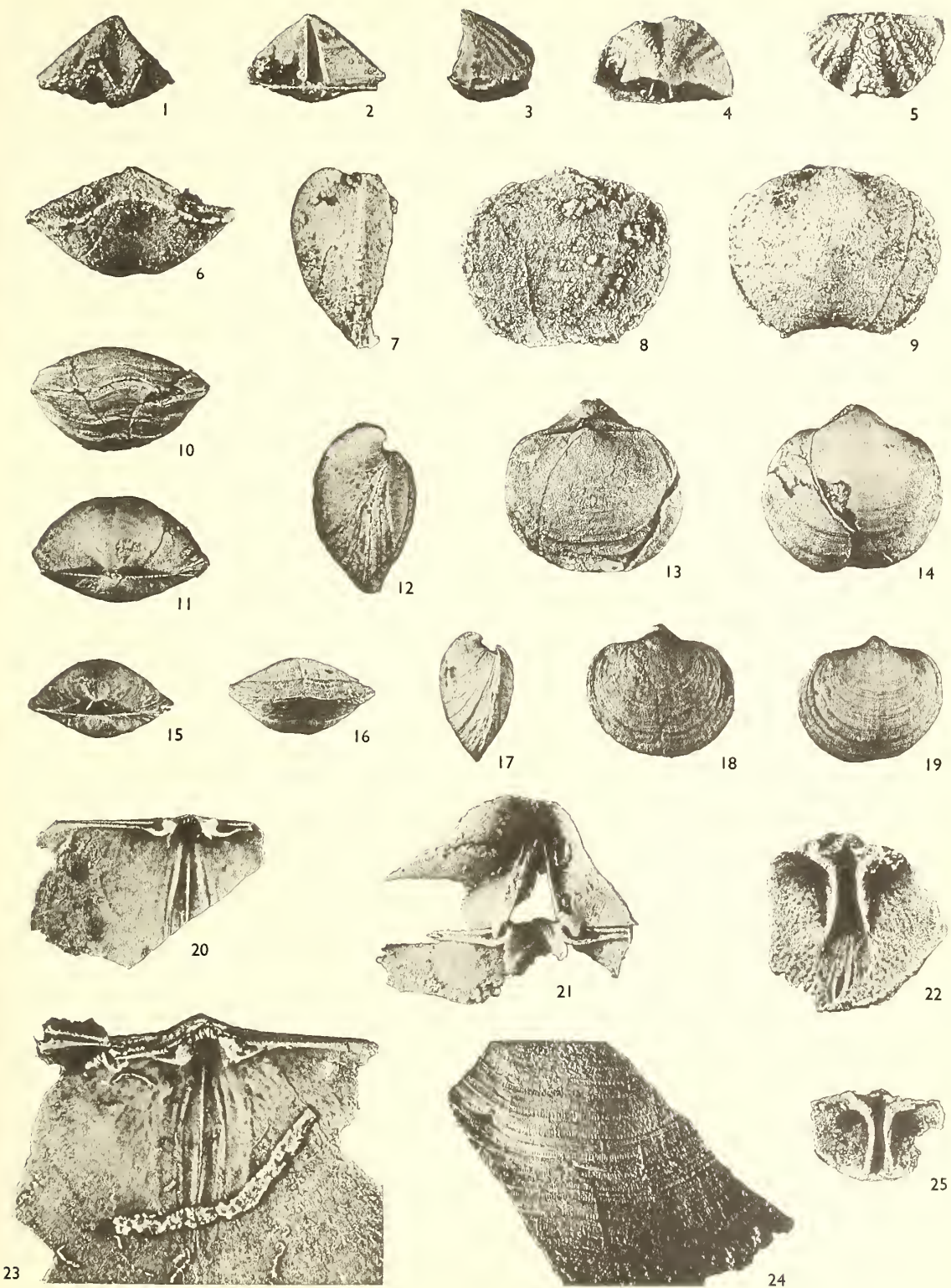


TEXT-FIG. 4. *Leptathyris circula*. *a*, Interior of pedicle valve from the Roberts Mountains with fragment of brachial valve retaining cardinal plate attached. *b*, Cardinalia of brachial valve of a paratype from Lone Mountain showing the shape of the cardinal plate and the apical foramen.

distance as ridges that bound the muscle impression. These ridges terminate anteriorly at about the place of constriction between the pedicle cavity and the diductor muscle scars. The diductors are faintly impressed, elongate, and slightly divergent. Medially there is a faintly elevated myophragm dividing the diductors into two more or less separate tracks that blend anteriorly with the interior of the valve (text-fig. 4).

EXPLANATION OF PLATE 27

- Figs. 1–5. *Cyrtina* sp. Lower *Leptathyris circula* zone, loc. 4739, northern Roberts Mountains. 1–5, Anterior, posterior, side, ventral, and dorsal views $\times 2$, USNM 145528.
- Figs. 6–9. *Warreuella* cf. *columbina columbina* (Havlíček 1959). Lower *Leptathyris circula* zone, loc. 4739, northern Roberts Mountains. 6–9, Anterior, side, dorsal, and ventral views $\times 3$, USNM 145529.
- Figs. 10–25. *Warreuella kirki praekirki* Johnson subsp. nov. Figs. 10–24, lower *Leptathyris circula* zone, loc. 4739, northern Roberts Mountains; fig. 25, zone unknown, loc. 4742, northern Roberts Mountains. 10–14, Anterior, posterior, side, dorsal, and ventral views $\times 1.5$, holotype, USNM 145530. 15–19, Posterior, anterior, side, dorsal, and ventral views $\times 2$, paratype, USNM 145531. 20, Interior of brachial valve $\times 4$, paratype, USNM 145532. 21, Interior of posterior portions of articulated fragments of both valves $\times 5$, paratype, USNM 145533. 22, Interior of fragment of pedicle valve $\times 3$, paratype, USNM 145534. 23, Interior of brachial valve $\times 4$, paratype, USNM 145535. 24, Exterior of fragment $\times 5$, paratype, USNM 145536. 25, Interior of fragment of pedicle valve $\times 2$, USNM 145537.



JOHNSON, Devonian brachiopods from Nevada

Interior of brachial valve. The sockets diverge antero-laterally and are unsupported by crural plates. Their inner edges are joined by an apically perforate cardinal plate which is slightly depressed dorsally across its width, but which is crested along the median line with its crest ventrally directed. In plan view the anterior edge of the cardinal plate is two sided, converging anteromedially. Neither median septum nor myophragm are present. The spiralia have their apices directed laterally and appear to consist commonly of six or eight turns.

Occurrence. *Leptathyris circula* is very common in the lower two or three hundred feet of the Denay Limestone at a number of places in the Roberts Mountains and in the northern Simpson Park Range. As reported previously (Johnson 1962a, p. 167) Merriam states that forms assignable to this species are present at the north end of the Antelope Range.

Suborder SPIRIFEROIDEA

Superfamily DELTHYRIACEA Phillips 1841

[*nom. transl.* Ivanova 1960 (*ex* Delthyridae Phillips 1841)]

Family RETICULARIIDAE Waagen 1883

[*nom. transl.* Ivanova 1960 (*ex* Reticulariinae Waagen 1883)]

Genus WARRENELLA Crickmay 1953

Type species. *W. eclecticæ* Crickmay 1953, p. 596, figs. 1-5, 16-19.

Warrenella kirki praekirki subsp. nov.

Plate 27, figs. 10-25

Material. The holotype is USNM no. 145530, illustrated in figs. 10-14 of Plate 27 and measures 19.2 mm. in width, 18.2 mm. in length, and 11.4 mm. in thickness. It was collected at locality 4739 on the west slope of Willow Creek Canyon in the northern Roberts Mountains. The remainder of the specimens illustrated on Plate 27 are paratypes excepting fig. 25 which originates from another locality. These include USNM nos. 145531-7.

Diagnosis. Includes relatively transverse, less strongly convex specimens of *W. kirki* in populations lacking elongate individuals.

Exterior. The shells are transversely suboval in outline and unequally biconvex in lateral profile with the pedicle valve about twice as strongly convex as the brachial valve. The hinge line is equal to about two-thirds the maximum width of the valves which is attained near midlength. The cardinal angles are rounded and obtuse. The pedicle valve bears a low apsacline triangular interarea with a relatively strongly incurved beak. The interarea is divided medially by a triangular open delthyrium enclosing an angle of about 70°. The interarea of the brachial valve is long, narrow, and anacline. The pedicle valve commonly bears an indistinct medial sulcus which may extend from the umbo or may develop anterior to it. The sulcus of all the specimens examined is relatively shallow and rounded, not angular. A fold is not developed on the brachial valve.

There are no radial plications. The concentric ornament consists of numerous very fine, concentric growth lines and a few more strongly accentuated ones, more commonly on the anterior of larger shells. The fine ornament consists of concentric rows of fine radial striae along the anterior edge of the growth lamellae, but not continuing back to the anterior edge of the previous growth lamellae.

Interior of pedicle valve. The hinge teeth are strong knob-like projections, directed dorsally and converging slightly postero-medially. They are supported basely by stout dental lamellae that initially converge slightly toward the midline and diverge slightly from it along their anterior edges. The dental lamellae are very closely set together at the umbo and constrict that space in most specimens making the pedicle cavity obsolescent. The ventral muscle scar is deeply impressed, triangular, and elongate with slightly divergent sides laterally and a semicircular outline anteriorly where it blends with the interior of the shell. The adductor muscle scars compose a pair of elongate raised ridge-like tracks medially which are separated by a subangular myophragm. On some specimens the adductor tracks appear to extend slightly anterior to the anterior edge of the elongate oval anterior portion of the diductor impressions.

Interior of brachial valve. The hinge plates define relatively strong, deep, subconical, and broadly divergent sockets that are attached beneath the inner edges of the dorsal interarea. Commonly, there is a small rim of shell material extending laterally from the distal end of the socket beneath the interarea and parallel to it. Medially the hinge plates bear a pair of triangular crural plates that are attached to the inner surface of the posterior end of the valve, but which are free of the floor of the valve along most of their length. The crural plates are relatively strongly concave on their inner (medial) faces and with their dorsal sides thus attaining a position subparallel to the interior of the umbo of the valve. Medially in the notothyrial cavity, the site of diductor attachment is composed of a deeply striate, transverse, comb-like process. The adductor muscle scars comprise two pairs of very elongate subelliptical impressions with the medial pair more deeply impressed and separated from the lateral pair by thin rounded ridges. The medial pair are divided by a thin low myophragm throughout most of their length.

Comparison. The new subspecies is distinguished from *Warrenella kirki kirki* by a more transverse outline and a less well-developed median sulcus in the pedicle valve of the former. A typical population of *W. kirki kirki* includes transverse specimens, but these commonly bear a relatively strong subangular sulcus. Included with these are an almost equal number of elongate suboval specimens. *W. kirki praekirki* appears to be the initial subspecies in Nevada, subject to a trend from transverse to elongate specimens. Some collections above *W. kirki kirki* contain an abundance of markedly elongate forms and lack of any of the transverse ones typical of the early forms or which are also found in the middle stratigraphic horizons. *W. occidentalis* is a very large transverse species with a relatively deep median sulcus which may be relatively flat-bottomed in some forms. In the writer's opinion, the Canadian species *W. franklini* is very close to the transverse forms of *kirki kirki* and may prove to be a senior synonym of that species. *W. occidentalis* may have been derived from the later form at a time when the typical *kirki kirki* gave rise to two species out of its diverse population.

Crickmay (1962, p. 10) has recently assigned his species *W. timetea* to the genus *Tingella* Grabau, because of the presence of crural plates. *Timetea* is very close to *occidentalis* of Nevada and may be conspecific, however, the writer has not studied large collections of the Canadian species. Specimens of *occidentalis* from Nevada also bear relatively large crural plates as do all the specimens assigned to *kirki* and its various subspecies discussed here. However, the writer is not convinced that the information on the structural details and external ornament of *Tingella* are well enough known to bring

that name into widespread usage in western North America. All of the reticulariid genera in the Devonian that the writer has studied from Nevada and including a number of species from both the Lower and Middle Devonian, bear crural plates that are attached to the base of the valve along varying percentages of their total length. It seems appropriate that the type species of *Warrenella* be much more closely studied with regard to the structure of the cardinalia to determine whether crural plates are present and buried in secondary shell material, or present and not in contact with the base of the valve, or are completely absent.

Grabau's only figured internal mould of *Tingella* (1933, pl. 43, fig. 7), in addition to showing long slots for the crural plates, also shows thin, discrete, widely spaced, dental lamellae in the pedicle valve and a muscle field that is not impressed. *W. kirki* typically bears dental lamellae that are closely set and adjoin umbonal cavities that bear considerable secondary shell material. This suggests to the writer that *W. kirki*, despite its well-developed crural plates, is not closely related to *Tingella*.

Warrenella appears to be a senior subjective synonym of *Minatothyris* Vandercammen 1957, which is based on a species from the Frasnian of western Europe (*Spirifer euryglossus* Schnur), a species which is in fact very close to the type of *Warrenella*. The latter genus, as viewed by the writer and discussed above, is also a senior subjective synonym of *Sinothyris* Minato 1953, which is based on the west European Givetian species *S. maureri* Holzapfel. This, on exterior considerations at least, appears to be a species relatively close to the group of *franklini*, *occidentalis*, and *timetea*. Vandercammen (1957) has already included *maureri* in *Minatothyris* and it is evident that Minato's conception of *Sinothyris* based on Grabau's illustration and description was erroneous since the type species lacks a ventral median septum.

Occurrence. *W. kirki praekirki* is at present known only from the *Leptathyris circula* zone in Eureka County, Nevada.

Warrenella cf. *columbina columbina* (Havlíček 1959)

Plate 27, figs. 6-9

1959 *Eomartiniopsis columbina columbina* Havlíček, p. 190, pl. 28, figs. 3-5.

Material figured. USNM no. 145529.

Exterior. The shells are transversely subquadrate in outline and strongly biconvex in lateral profile with the pedicle valve more strongly so than the brachial valve. The beak on the pedicle valve is relatively short and stubby. The hinge line is short and straight medially and there is a narrow triangular apsacline interarea, slightly incurved near the beak, and equal to a little less than half the maximum width of the valves. The interarea is cleft medially by a triangular open delthyrium enclosing an angle 55-60°. The umbo on the brachial valve is relatively prominent, strongly convex, and the beak is strongly incurved. The cardinal angles are obtuse and strongly rounded. The maximum width is posterior to the midlength and the antero-lateral margins slope forward and converge slightly toward the midline. There is a deep subangular sulcus on the pedicle valve, originating near the umbo and becoming decidedly stronger and flaring in width toward the anterior commissure. The brachial valve bears a rounded fold that is faintly marked off from the lateral portions of the valve.

The ornament consists of numerous fine concentric growth lines. The fine radial ornament, if present, was not detected due to inadequate preservation.

Interior of pedicle valve. There are a pair of short thick dental lamellae in the apex of the valve that diverge only slightly from one another and which are situated very close together at the beak. The diductor scar consists of a triangular, faintly impressed area which blends anteriorly with the interior of the valve. The umbonal cavities are free of infilling secondary shell material.

Occurrence. The species appears at two localities in the *Leptathyris circula* zone on the north side of the Roberts Mountains and in a single collection from Lone Mountain which also contains specimens of *Warrenella kirki praekirki*.

Family AMBOCOELIIDAE George 1931

[*nom. transl.* Ivanova 1960 (*ex Ambocoeliinae* George 1931)]

Genus ECHINOCOELIA Cooper and Williams 1935

Type species. *E. ambocoelioides* Cooper and Williams 1935, p. 844, pl. 59, figs. 9, 13, 17, 21, 23.

Echinocoelia denayensis sp. nov.

Plate 26, figs. 23–30

Material. The specimen, USNM no. 145527, illustrated in figs. 26–30 of Plate 26 is the holotype. It measures 9.0 mm. in width, 8.0 mm. in length, and 7.6 mm. in thickness. Other figured specimens include USNM nos. 145524–6.

Diagnosis. *Echinocoelia* with typical form, but with rudimentary, anteriorly free, crural plates.

Exterior. The shells are subtrigonal in outline and strongly unequally biconvex, pyramidal in lateral profile. The brachial valve is only gently curved, nearly flat and cap-like. The pedicle valve is deeply convex and strongly arched with a high, steeply apsacline to nearly catacline, only slightly incurved interarea which is equal to about three-quarters of the maximum width of the valves. It is cleft medially by a high, triangular, open delthyrium that encompasses an angle of about 30°. The interarea on the brachial valve is long, low, and anacline. Most specimens are transverse, but become less so with an increase in size. The outline of larger specimens, especially brachial valves, is somewhat pentagonal with the maximum width well posterior to midlength and with the sides sloping antero-medially and truncated by a short anterior commissure at right angles to the median plane. No fold or sulcus is developed on the pedicle valve but a very faint flattening or depression of the interior edge of the brachial valve causes the anterior commissure to be deflected slightly ventrally.

The valves are without plication but develop a fairly strongly lamellose ornament of concentric growth lines that are very numerous and closely set and which are more pronounced at a few irregular intervals. Preservation of the fine ornament is imperfect, but on the best preserved specimens it appears to consist of extremely fine radial striae situated in concentric rows on the growth lamellae.

Interior of pedicle valve. The hinge teeth are small, thin, elliptical processes which project dorsally from the base of the hinge line and have their long axes approximately midway

between the hinge line and the median plane. The hinge teeth leave small ridge-like tracks on the inner edges of the delthyrium. There are no dental lamellae. The apex of the delthyrium is closed by a small plate.

Interior of brachial valve. The sockets are broad, shallow, and widely divergent antero-laterally. They are attached on their medial edges to relatively large triangular crural plates which contact the interior surface of the valve posteriorly, but which are free anteriorly. Medially there is a small knob-like cardinal process in the apex of the notothyrium. Commonly there is a long, low, narrow myophragm running most of the length of the valve. The adductor muscle scars, however, are not impressed. Commonly, on the more lamellose brachial valves, the interior is strongly crenulated in the anterior half of the shell by the concentric undulations of the more prominent growth lamellae.

Occurrence. *Echinocoelia denayensis* is a common species in the *Leptathyris circula* zone on the north side of the Roberts Mountains as well as on the west slope, east of Red Canyon. This species is also present in the *L. circula* zone in the northern Simpson Park Range.

Comparison. *Echinocoelia ambocoelioides* Cooper and Williams (1935, p. 844, pl. 59) has a more pyriform outline than *E. denayensis* and long crural plates, lacking in the latter species. The new species is very close to *E. incurva* Cooper and Williams (1935, p. 845, pl. 59, figs. 20, 24, 25) but has a more nearly catacline palintrope and intermittantly coarse concentric growth lines. The interior of *E. incurva* is unfortunately not known. *E. denayensis* very closely resembles *Ambocoelia rogeri* Drot (1955, p. 565, pl. 27, fig. 3a-d). Drot (p. 566) mentions the presence of a septum (= ?myophragm) in the brachial valve, but excludes her new species from *Echinocoelia* which it resembles in most characters. *E. denayensis* differs from *E. ? rogeri* in having a relatively flatter brachial valve that bears a less well pronounced ventral deflection of its anterior commissure. The palintrope of *E. ? rogeri* is less incurved at the beak and there are some minor differences in surface ornament as a comparison of the illustrated specimens will indicate, but it is not certain what value these may have.

Superfamily CYRTINACEA Fredericks 1912

[*nom. transl.* Johnson herein]

Discussion. Inclusion of the cyrtinids in the Spiriferaceae has been suggested (Ivanova 1960, p. 278), however, such an assignment should not be taken to indicate more than a morphologic grouping of the punctate Spiriferoidea. If phylogenetic implications were assumed, this procedure would require *Spiriferina* and its allies to have been derived from *Cyrtina*, a connexion regarded as improbable by the writer since *Cyrtina* possessed a more specialized morphology, exemplified by its tichorhinum and stout apically perforate deltidium, long before the appearance of the more generalized spiriferinaceids. *Cyrtina* appeared at or near the beginning of the Early Devonian and represented a major new stock contrasting markedly with the then existing Cyrtiidae (the eospiriferids) and the Delthyridae (principally *Delthyris* and *Howellella*).

Family CYRTINIDAE Fredericks 1912

[*nom. transl.* Stehli 1954 (*ex* Cyrtininae Fredericks 1912)]

Genus CYRTINA Davidson 1858

Type species. *Calceole heteroclite* Defrance 1824, p. 306, pl. 80, figs. 3, 3a.

Cyrtina sp.

Plate 27, figs. 1-5

Material figured. USNM no. 145528.

Exterior. The shells are transversely subtrigonal to sub-semicircular in outline and strongly unequally biconvex in lateral profile. The pedicle valve is strongly convex, subpyramidal, and the brachial valve is gently convex and cap-like. The pedicle valve bears a high, nearly flat, catacline, triangular interarea cleft medially by a long delthyrium enclosing an angle of about 20°. The deltidium is not preserved. There is a shallow subangular sulcus on the pedicle valve and a corresponding strong rounded fold on the brachial valve and three or four rounded plications on each flank of the valves separated by shallow U-shaped interspaces.

Occurrence. *Cyrtina sp.* is present, but not common in the *Leptathyris circula* zone on the north side of the Roberts Mountains.

APPENDIX OF LOCALITIES

The numbers listed below are those of the locality register of the Department of Geology, University of California, Los Angeles.

3536 North-east slope of Union Mtn., north-east of McColley Canyon, elev. 6,825, 900 ft. W., 3,350 ft. N. of SE. cor. of sec. 20, T. 27N., R. 53E., Mineral Hill quad., Sulphur Spring Range, Elko Co., Nevada. Telegraph Canyon Member of Nevada Fm. (Carlisle *et al.* 1957).

4737 Approx. 4,500 ft. due E. of Roberts Creek on small spur on south slope of hill 7964, elev. 7,420, sec. 1 (unsurveyed) T. 22N., R. 50E., Roberts Creek Mtn. quad., Roberts Mts., Eureka Co., Nevada. Denay Ls., M. Dev., 20-50 ft. above top of McColley Canyon Fm. Collector: E. L. Winterer, 1959.

4738 Approx. 3,300 ft. due E. of Roberts Creek, elev. 6,920, eastward across canyon from hill 6963, 7,400 ft. almost due N. of NE. cor. sec. 24, T. 22N., R. 50E. Roberts Creek Mtn. quad., Roberts Mts., Eureka Co., Nevada. Denay Ls., M. Dev., about 300 ft. above top of McColley Canyon Fm. Collector: E. L. Winterer, 1959.

4739 Approx. 3,200 ft. due W. of Willow Creek, elev. 7,520, at crest of ridge between Willow Creek and Birch Creek, 4,200 ft. south of SE. cor. of sec. 22, T. 24N., R. 50E., Roberts Creek Mtn. quad., northern Roberts Mts., Eureka Co., Nevada. Denay Ls., M. Dev., approx. 170 ft. above top of McColley Canyon Fm. Collectors: Student group 11, 1958 and J. G. Johnson, 1959.

4740 East of Willow Creek, elev. 6,900 ft., 2,800 ft. E., 3,700 ft. S. of SE. cor. of sec. 15, T. 24N., R. 50E., Roberts Creek Mtn. quad., northern Roberts Mts., Eureka Co., Nevada. Lower Denay Ls., M. Dev. Collector: J. G. Johnson, 1959.

4741 Elev. approx. 6,800 ft., on east flank of Willow Creek, approx. 6,500 ft. upstream from Willow Creek Ranch, 1,900 ft. S., 2,300 ft. E. of SE. cor. of sec. 22, T. 24N., R. 50E., Roberts Creek Mtn. quad., northern Roberts Mts., Eureka Co., Nevada. Denay Ls., M. Dev. Collector: J. G. Johnson, 1959.

4742 South flank of Hanson Creek, north of Red Canyon, elev. 7,320 ft., 7,900 ft. due E. of SE. cor. of sec. 1, T. 23N., R. 49E., west slope of Roberts Creek Mtn., Roberts Creek Mtn. quad., Eureka Co., Nevada. Denay Limestone, M. Dev. Collectors: Student group 14, 1958.

4743 South-west slope of hill 8919, east of Red Canyon, elev. 8,040 ft., 10,400 ft. E., approx. 1,200 ft. S. of SE. cor. of sec. 12, T. 23N., R. 49E., Roberts Creek Mtn. quad., Eureka Co., Nevada. Denay Limestone. M. Dev. Collector: unknown.

4744 Elev. 7,880 ft., head of Birch Creek, crest of ridge c. 5,500 ft. NNW. of Cooper Peak, and c. 9,100 ft. ESE. of Western Peak, T. 23N., R. 50E., northern Roberts Mts., Roberts Creek Mtn. quad., Eureka Co., Nevada. Denay Limestone, M. Dev. Collector: M. A. Murphy, 1957.

4745 Elev. 8,640 ft. east slope of saddle 500 ft. N. of hill 8788, approx. 3 miles W. and 3 miles N. of Roberts Creek Ranch, T. 22N., R. 50E., southern Roberts Mts. west of Roberts Creek, Roberts Creek Mtn. quad., Eureka Co., Nevada. Denay Limestone, M. Dev. Collector: E. L. Winterer, 1959.

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A REVISION OF *ACASTE DOWNINGIAE* (MURCHISON) AND RELATED TRILOBITES

by J. H. SHERGOLD

ABSTRACT. Three species of *Acaste*, *A. downingiae* (Murchison), *A. inflata* (Salter), and *A. subcaudata* (Murchison); two species of *Acastocephala* gen. nov., *A. macrops* (Salter) and *A. dudleyensis* sp. nov.; and *Acastoides constricta* (Salter) are described from rocks of Wenlockian age from the West Midlands, Welsh Borderlands, and South Wales. Their relationships to later Silurian and early Devonian acastomorph genera are discussed.

THE species *Calymene? downingiae* was first recognized by Murchison (1839) who divided it from *Calymene macrophthalma* Brongniart on account of its smaller eyes and well-developed glabellar furrows. The species was subsequently placed in the genus *Phacops* by Emmerich (1845) and by Salter (1848, 1853), M'Coy (1851), and Murchison (1859). Goldfuss (1843) established the genus *Acaste*, which was regarded as a subgenus of *Phacops* by Salter (1864). *Acaste downingiae* was the first of a group of eight species listed by Goldfuss (1843, p. 563) and has been regarded by subsequent authors as the type species although this was not definitely established until 1959 (Struve in Moore, 1959, p. O488). R. Richter (1909) and R. and E. Richter (1939, 1952, 1954) discussed the morphology, relationships, and successions of acastomorph trilobites but concentrated their attention mainly on Devonian genera.

Salter (1864) divided the species into six varieties which he distinguished by Greek letters. At the present time these are assigned to the following taxa. After the revision of R. and E. Richter (1954, p. 16) var. α , *vulgaris* becomes *Acaste downingiae* (Murchison) s.s. and var. ϵ , *constrictus* is assigned to the genus *Acastoides* Delo 1935, becoming *A. constricta* (Salter). Var. δ , *spinosus* was chosen by Reed in 1925 as the type species of *Acastella*. Two further varieties are revised below. Var. γ , *inflatus* has been retained in the genus *Acaste* as *A. inflata* (Salter). For trilobites previously referred to var. β , *macrops* a new genus, *Acastocephala*, has been erected to include two species, *A. macrops* (Salter), the type species and *A. dudleyensis* sp. nov. Salter's var. ζ , *cuneatus*, based on a poorly preserved cephalon from the Denbigh Grits of Llanrwst, is the only specimen known from that area and until further material becomes available cannot be adequately described.

The present paper is based mainly on materials from the Wenlockian of the West Midlands, Welsh Borderlands, and South Wales in the following collections: the Sedgwick Museum, Cambridge (SM); Oxford University Museum (OUM); Birmingham University Museum (BU); the British Museum (Nat. Hist.) (BM); the Geological Survey Museum (GSM); the Geological Society Collection (GSC); and the National Museum of Wales (NMW). Additional material has been used from the Bristol City Museum; the Ludlow Museum; the Hancock Museum, Newcastle upon Tyne; the Departmental Collections, University of Newcastle upon Tyne (UNT), and from collections made by the author in South Wales.

Relationships of considered genera. Struve (1958b) has used the term 'acastomorphen' for Phacopacea with dalmanitid tendencies as distinct from those with calmonioid tendencies. The writer has here used the term in a somewhat different sense to include

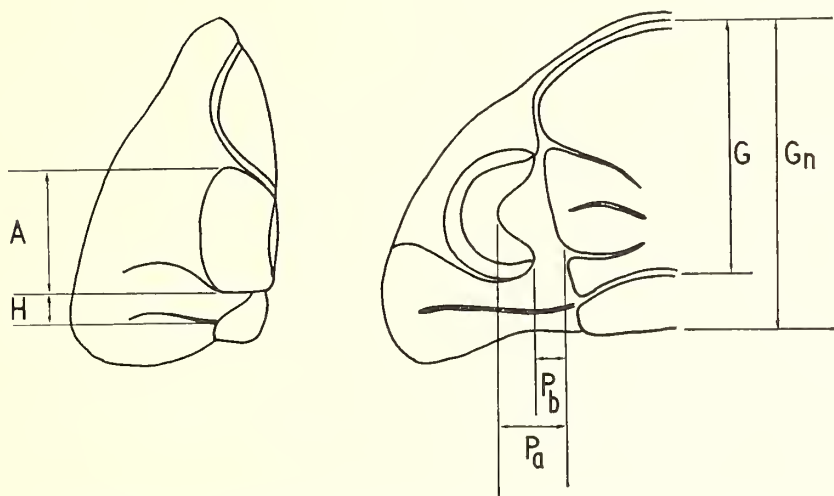
[Palaeontology, Vol. 9, Part 2, 1966, pp. 183-207, pls. 28-32.]

the genera *Acaste*, *Acastoides*, *Acastella*, *Acastellina* R. and E. Richter 1954, *Acastava* R. and E. Richter 1954, and *Acastocephala* gen. nov., feeling that these genera form a closely related Siluro-Devonian complex. In Struve's (1958b, 1959) current classification these genera are grouped into two subfamilies, Acastinae Delo 1935 and Acastavinae Struve 1958. The former is included in the family Calmoniidae and the latter in the Dalmanitidae. The Acastavinae (*Acastava*, *Acastella*, and *Acastellina*) are thought by Struve to show an asteropyginid trend in certain characters, namely the shape of the cephalon, the construction of the genal spines and the poorly segmented pygidium with its marked tendency to develop denticulations along the lateral margins. The Acastinae, while including such genera as *Acaste* and *Acastoides*, embraces also *Scotiella* and *Phacopina*, subgenera in which the glabellar segmentation has become faint or obsolete. The mucronations possessed by members of the Acastinae are thought by Struve to be essentially similar in construction to the Calmoniidae rather than the Dalmanitidae.

During the early holaspid ontogeny of *Acaste downingiae* and *A. subcaudata*, short but distinct genal projections are observed on the posterolateral fixigenal margins. These projections, in effect miniature spines, are rapidly resorbed in succeeding moults. In their construction these spines differ from those produced by the Dalmanitinae and Asteropyginae which are massive continuations of the cephalic margins but are more similar to the small, elegant mucronations shown by such typical calmoniid genera as *Bainella*, *Schizostylus*, and *Paracalmonia* or to those of the acastavinid genus, *Acastella*. In their orientation these small acastid spines contrast with those of the Calmoniidae which are deflected prominently outwards from the line of the cephalic margin, but compare well with those of the Acastavinae, being most closely comparable with the mucronations displayed by the adult of *Acastella prima* Tomczykowa (1962a, pp. 261-2, pl. 1, figs. 2, 4, 5). If the early holaspid mucronations of *Acaste downingiae* were to be continued into the adult stage the condition of *Acastella prima* would be closely approximated (text-fig. 3). The derivation of *Acastella* from *Acaste* through an intermediate form such as *Acastella prima* becomes a strong probability (Tomczykowa 1962b, p. 202).

Acastocephala dudleyensis sp. nov. also possesses small genal mucronations in its early holaspid ontogeny. In the adult condition these are again resorbed and the genae become posterolaterally angled or rounded. The construction and orientation of these spines are essentially similar to the condition shown by the adult of *Acastava atava* (W. E. Schmidt 1907). Further similarities are shown between *Acastocephala* and *Acastava*, for the lateral pygidial margins of young holaspides in both *Acastocephala macrops* and *A. dudleyensis* are provided with three or four pairs of denticulations on the external surface of the shell, similar to those found on the internal mould of the adult *Acastava atava* (text-fig. 5). As with the genal spines, these denticulations are resorbed in the adult which possesses a typically entire margin. Young holaspides, therefore, show the asteropyginid trend of Struve, while the adults with rounded genae and entire pygidial margins do not. In other characters, notably the size and position of the eye and the poorly segmented pygidium, adults of *Acastocephala macrops* are closely comparable to *Acastava atava*. It appears, therefore, that the conditions shown by the early holaspides of *Acastocephala* are retained into the adult stages of *Acastava*. Accordingly *Acastocephala* is thought to be ancestral to *Acastava* and is classified with the Acastavinae.

Two lines of development may thus be postulated among the acastomorph genera. *Acastava* (Siegenian–Emsian) may be derived from *Acastocephala* (Wenlockian) and *Acastella* (Middle Ludlow–?Siegenian) from *Acaste* (Wenlockian–L. Gedinnian). The various Silurian and Devonian species of *Acastoides* (Wenlockian–U. Emsian) appear to be a closely related and distinct group, isolated from other lines of development from Wenlockian times onwards.



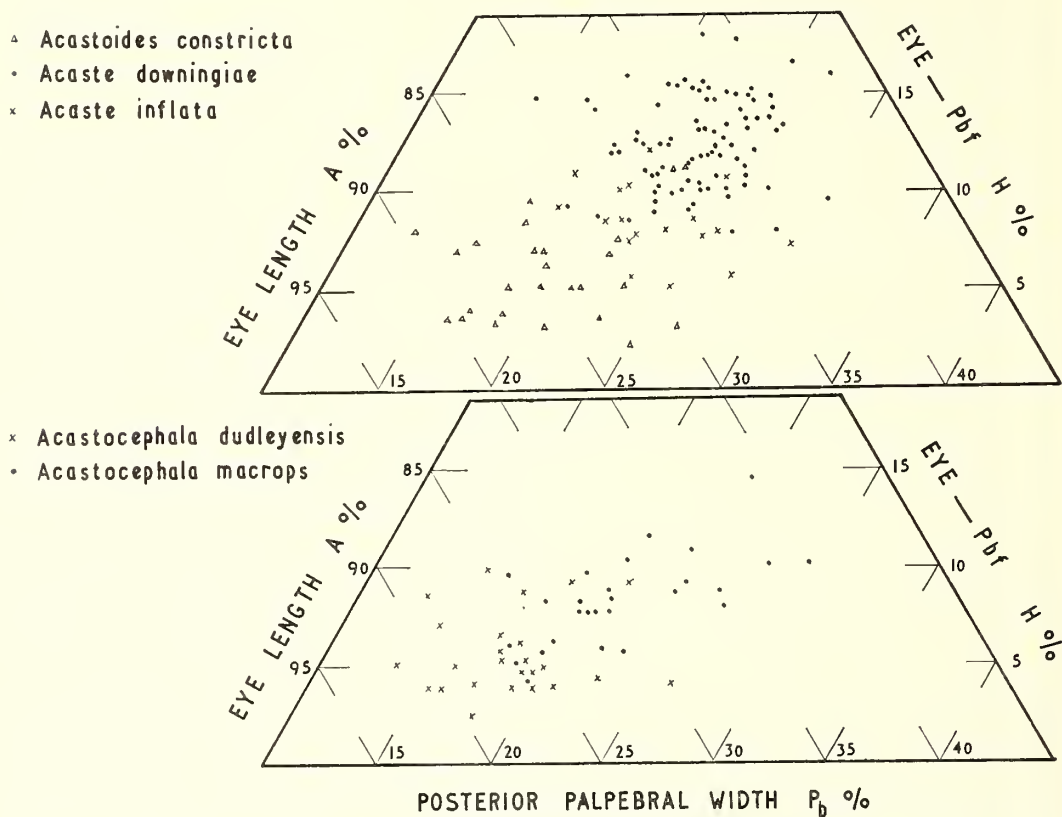
TEXT-FIG. 1. Parameters recorded on a typical acastomorph cephalon.

Measurements. Measurements based on the lengths and widths of the cephalon, thorax and pygidium have been found to be extremely variable and to be largely dependent on preservation. Selected measurements connected with the eye, on the other hand, have shown constancy both intra-generically and intra-specifically. The position of the eye on the cheek with relation to the cephalic margins, posterior border furrow and glabella and the differing relationships between eye length and glabellar length are important in this respect.

The measurements recorded are basically those of Struve (text-fig. 1). They are essentially the eye length, A ; glabellar length, G ; occipital glabellar length, G_n ; and a measurement, H , across the posterior fixigena between the back of the eye and the posterior border furrow. In addition to Struve's parameters, the maximum width, P_a , and the posterior width, P_b , across the palpebral area have been recorded. Of these latter measurements, P_a has been found to depend upon the definition of the palpebral furrow and to be more variable than P_b (see text-fig. 1).

After Struve (1958*a*), several ratios have been considered important. A/G , the larger eye index; A/G_n , the smaller eye index, and H/A have been used to give some idea of the eye length in relation to glabellar length and the distance of the eye from the posterior border furrow. Values of H/A have shown that in some species the eye remains in a more or less constant position during holaspide ontogeny, while in others it appears to migrate in a posterior direction (see section under *Acastocephala dudleyensis*).

In the text the following glabellar notation is used; preoccipital lobe, 1L; median lateral lobe, 2L; anterior lateral lobe, 3L; 1S, 2S, and 3S are the equivalent glabellar side furrows.



TEXT-FIG. 2. The position of the eye on the cheek plotted with reference to the eye length, posterior border furrow and distance of the eye from the posterior border furrow.

Generic and Specific Differentiation. Characters considered to be of generic importance are as follows: the shapes of both cephalon and pygidium, i.e. the geometry of outline; the segmentation of the pygidium, both in axial and pleural elements; and the size of the eye and its position on the cheek. To illustrate the position of the eye and its relative size the proportionate relationships between A, H, and Pb have been plotted on triangular-based graph paper (text-fig. 2). Further, the development during ontogeny of genal mucronations and pygidial denticulations is of fundamental importance.

Of importance specifically are the convexities (tr. and sag.) of the frontal lobe, 1L and the occipital ring; the height to which the occipital ring is raised above the glabellar side lobes; the shape, in plan view, of the glabella; the number of facets at the maximum height of the visual surface; the convexity (tr.) of the pygidium, both pleural and axial elements; and the width of the pygidial border.

SYSTEMATIC DESCRIPTIONS

Family CALMONIIDAE Delo 1935

Subfamily ACASTINAE Delo 1935

Genus ACASTE Goldfuss 1843

Acaste downingiae (Murchison 1839)

Plate 28, figs. 1–18; Plate 29, figs. 1–8

1839 *Calymene* ? *Downingiae* (n.s.) Murchison, p. 655, pl. 14, figs. 3a (BU 54) and 3b (specimen untraced).

1851 *Phacops Downingiae* (Murchison sp.); M'Coy, p. 160 (SM A28766).

1853 *Phacops Downingiae* Murchison; Salter, pp. 1–12, pl. 1, figs. 1 (BM 44252), 2 (untraced), 4 (GSM 19305), 5–13 (untraced), 15 (untraced).

1864 *Phacops (Acaste) Downingiae* Murchison, var. α , *vulgaris* Salter, p. 26, pl. 2, figs. 17 (BM 44407), 18 (BU 54), 19–22 (untraced), 23 (BM 44409), 25 (BU 129), also an unnumbered ventral surface between figs. 25 and 34 (BM 44410).

1864 *Phacops (Acaste) Downingiae* Murchison, var. γ , *inflatus* Salter, p. 27, pl. 2, figs. 31 (GSM 19305) and 33 (GSM 19306).

1954 *Acaste (Acaste) downingiae* (Murchison 1839); R. and E. Richter, pp. 16–17, pl. 3, figs. 36 (BM In36153), 37–41.

1965 *Acaste downingiae* (Murchison 1839); Clarkson, p. 11, pls. 1, 2, pl. 3, figs. 1–3.

Lectotype (here designated). Murchison 1839, pl. 14, fig. 3a, BU 54, figured here, pl. 28, fig. 1. Wenlock Limestone, Wren's Nest, Dudley, Worcs.

Diagnosis. A species of *Acaste* with frontal lobe anteriorly depressed and glabellar lobes in general with low convexity (both tr. and sag.). Fixigenae of young holaspides with short, stout mucronate projections which are rapidly resorbed in the succeeding moults to give prominent angulations, these becoming less apparent with further increase in size. Visual surface of eye carrying columns of 8 (rarely 9) lenses alternating with 7 (rarely 8) at the maximum height. Pygidium with 7–9 axial segments, 6–7 pleural segments. In young, pleural field and border area more or less continuous, becoming separated in adult specimens by a shallow furrow or flattening.

Description. Cephalon subtriangular in outline, with narrow, triangular area of librigena projecting in front of the glabella. Surface of test with fine granules. Length of cephalon approximately $\frac{1}{2}$ – $\frac{2}{3}$ width.

Glabella anteriorly rounded, laterally sub-parallel, transverse width decreasing gradually and evenly to posterior; the axial furrows curving very gently round 2L and 3L. Glabella apparently more parallel-sided in large adults than in younger stages. Frontal lobe rounded both anteriorly and antero-laterally, with low to moderate convexity when viewed in lateral profile, large adult specimens having a somewhat greater convexity than immature specimens. 2L and 3L approximately equal in size, with slightly less convexity (trans.) than frontal lobe; abaxially fused. 1L about half as wide (exsag.) as 2L, with little greater convexity (tr.). 3S long, shallow, sigmoidal even in smallest specimens, with a marked posterior median deflection becoming gradually less distinct during ontogeny. 2S shorter than 3S, impressed to a similar depth, transverse or gently curved, with a faint posterior median deflection most pronounced in young forms; failing laterally to reach the axial furrows. 1S wider and deeper than 2S, of similar

length, deflected both medianly and abaxially to the anterior, becoming more transverse, less wide (exsag.) and less deep in later ontogenetic stages. All furrows reaching to within approximately equal distance of the sagittal line. Short median furrow on sagittal line typically present, extending from median extremities of 3S to about one quarter of the length of the frontal lobe.

Occipital furrow abaxially deeper than 1S, becoming shallow but remaining well defined sagittally. Occipital ring narrow (sag.), with slightly less transverse width but greater transverse convexity than 1L; in lateral profile raised slightly above glabellar side lobes at all stages of growth.

Genae gently sloping to a poorly defined border which passes antero-laterally into a narrow (sag.) triangular area of librigena forming the anterior margin of the cephalon. Preglabellar furrow narrow (sag.), shallow. Postocular section of facial suture cutting lateral cephalic margin opposite 1S or mid 2L; preocular section dorsal intramarginal, separating preglabellar furrow from anterior cephalic margin. Fixigenae in smallest holaspides produced postero-laterally into short, stout mucronate projections which in

EXPLANATION OF PLATE 28

Figs. 1–18. *Acaste downingiae* (Murchison 1839). 1, 2. BU 54; figured Murchison 1839, pl. 14, fig. 3a; Salter 1864, pl. 2, fig. 18. Wenlock Limestone, Dudley, Worcs. 1, General view, lectotype arrowed, $\times 1$. 2, Lectotype, cranium, $\times 2$. 3. BU 129; cephalon possibly figured Murchison 1839, pl. 14, fig. 3a (discussed R. and E. Richter 1954, pp. 16–17); Salter 1864, pl. 2, fig. 25. Wenlock Limestone, Dudley, Worcs. Dorsal view of cephalon, $\times 3$. 4–8. BM 44407; figured Salter 1864, pl. 2, fig. 17. Wenlock Limestone, Dudley, Worcs. 4, General view, $\times 1$. 5, Detail, dorsal view of cephalon, $\times 2$. 6, Dorsal view of pygidium and thorax, $\times 2$. 7, Lateral view of cephalon, $\times 2$. 8, Eye showing lens cavities, $\times 8$. 9. BU 129; Eye, $\times 8$. 10–12. GSM 19306; figured Salter 1853, pl. 1, fig. 15 and 1864, pl. 2, fig. 33. Wenlock Limestone, Eastnor, nr. Ledbury, Herefordshire. 10, Lateral view, $\times 3$. 11, Adult pygidium showing border furrow, dorsal view, $\times 3$. 12, View from posterior, $\times 3$. 13–14. GSM 19313; Adult pygidium, Wenlock Limestone, Dudley, Worcs. 13, Dorsal view showing border furrow, $\times 2$. 14, View from posterior, $\times 2$. 15–17. BM 44410; ventral surface figured Salter 1864, pl. 2, no figure number given. Wenlock Limestone, Dudley, Worcs. 15, General view, $\times 2$. 16, Hypostome, $\times 6$. 17, Articulation of posterior five thoracic segments and pygidium (on left), $\times 8$. 18. BM 44252; dorsal exoskeleton, figured Salter 1853, pl. 7, fig. 1. Wenlock Limestone, Dudley, Worcs. $\times 2$.

EXPLANATION OF PLATE 29

Figs. 1–8. *Acaste downingiae* (Murchison 1839). 1. BM 44409; cephalo-thorax figured Salter 1864, pl. 2, fig. 23. Wenlock Limestone, Dudley, Worcs. $\times 2$. 2–3. SM A28717; Wenlock Limestone, Dudley, Worcs. 2, Dorsal view of juvenile pygidium without border furrow, $\times 3$. 3, View from posterior, $\times 3$. 4–6. SM A28744; Wenlock Limestone, Dudley, Worcs. 4, Dorsal view of young holaspide showing genal projection, $\times 4$. 5, Lateral view, $\times 4$. 6, Genal angle, $\times 8$. 7. NMW G.391.2; Wenlock Limestone, Dudley, Worcs. Enlargement of genal angle showing resorption of genal projection, the stage succeeding that of fig. 6, $\times 8$.
Fig. 8. *Acaste?* *downingiae* (Murchison 1839). GSM 19305; glabella figured Salter 1853, pl. 1, fig. 4, and 1864, pl. 2, fig. 31. Wenlock Limestone, Ledbury, Herefordshire. Dorsal view, $\times 2$.
Figs. 9–16. *Acaste inflata* (Salter 1864). 9–14. OUM C9; Lectotype; figured Salter 1864, pl. 2, fig. 30. Wenlock Limestone, Ledbury, Herefordshire. 9, Dorsal view of cephalon, $\times 3$. 10, Lateral view, $\times 3$. 11, Dorsal view of pygidium, $\times 3$. 12, Posterior view of glabella showing convexities of 2L, 1L, and the occipital ring, $\times 4$. 13, Eye, $\times 8$. 14, Posterior view of pygidium, $\times 3$. 15–16. BM In36154; Wenlock Limestone, Dudley, Worcs. 15, Dorsal view of pygidium, $\times 3$. 16, Posterior view of pygidium, $\times 3$.



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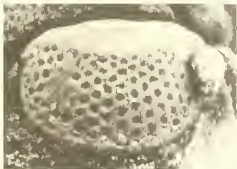
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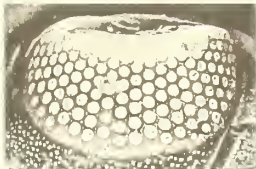
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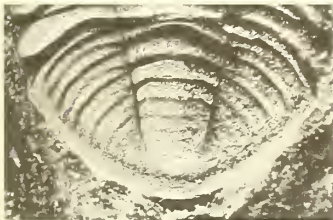
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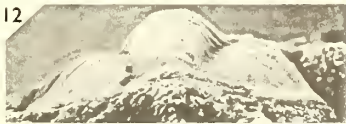
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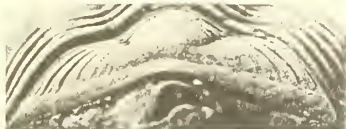
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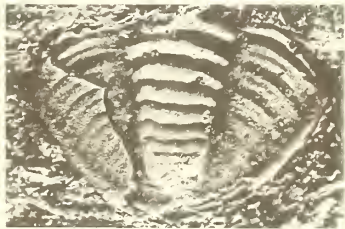
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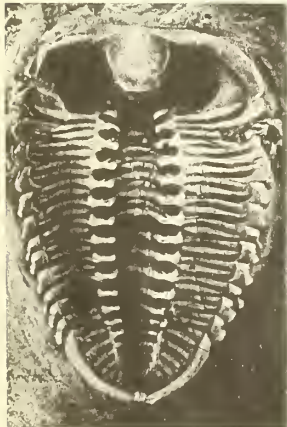
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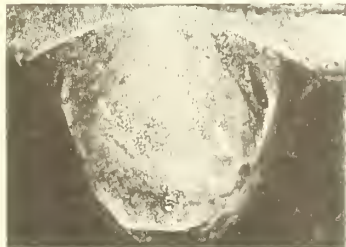
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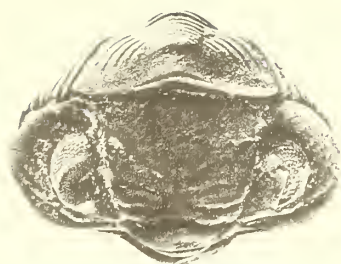
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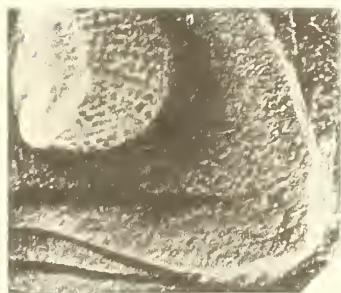
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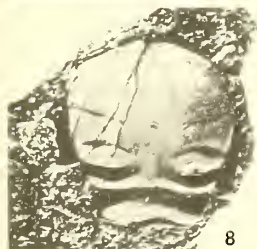
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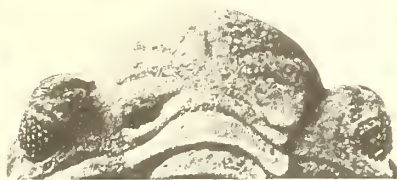
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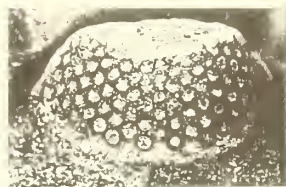
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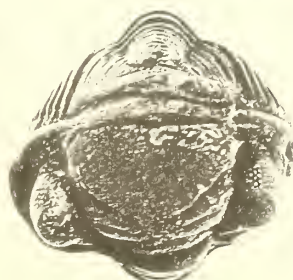
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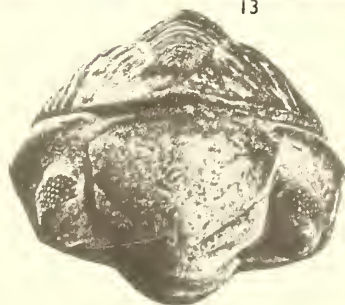
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the succeeding stages become gradually resorbed to give the angled adult condition (see below). Posterior border furrow transverse, deep but narrow (exsag.).

Eyes crescentic in plan, situated centrally between cephalic margin and glabella, on low ocular platform; extending from middle of 1L to anterior edge of 3L or to 3S; A/G, 46–67 per cent.; A/Gn, 37–54 per cent. Postocular area of fixigena relatively large, H/A 12–30 per cent. In lateral profile top of eye sloping gently to anterior; in anterior profile, well below surface of glabella. Palpebral lobes high; palpebral furrows generally well defined; palpebral areas relatively wide, with low inclination to axial furrows.

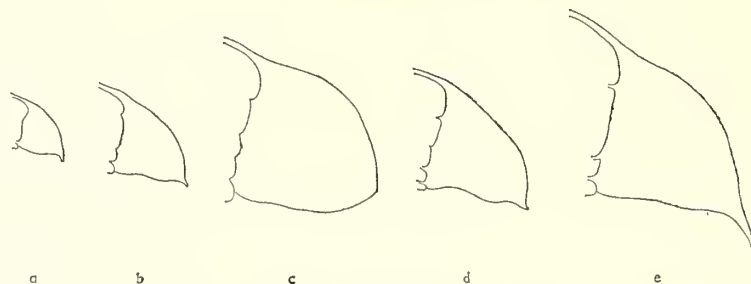
Visual surface overhanging slightly the ocular platform; gently convex or plane outwards; sloping more steeply outward-backwards than outward-forwards. Up to 168 lenses arranged in roughly alternating vertical columns containing at the maximum height of the surface 7 (8) or 8 (9) individual lenses, typically rounded or polygonal in outline and with a diameter of 0.2–0.255 mm. Interspaces granular, the granules arranged in a rough hexagonal network.

Hypostome subquadrate, anteriorly rounded, antero-laterally extended into short wings. Posterior margin straight, postero-lateral corners truncated. Lateral borders narrow, flat; posterior border more extensive. Median body adventrally convex, without distinct median furrow. Maculae forming small indistinct patches in anterior half of median body, close to lateral borders. Surface granulose.

Pygidium subtriangular in outline, margin entire at all growth stages; in posterior profile slightly vaulted; in lateral profile posterior margin curving gently addorsally. Axis raised above axial furrows and pleurae, moderately convex; composed of 8 axial segments in young, 8 (rarely 9) in adults, tapering to posterior and with a rounded, unsegmented terminal piece; segments 1–3 well defined, with strong transverse furrows; remaining segments becoming gradually less distinct to posterior. Pleurae moderately convex; 5 or 6 in young, 6 (rarely a trace of a seventh) in adults. Pleural furrows strong, interpleural furrows apart from the first, much weaker. Border wide at all growth stages. In young and juvenile forms the border is a smooth, unfurrowed extension of the pleural area but specimens with a pygidial length of 7.50 mm. and greater rapidly develop a flattening or shallow furrow at the junction of border and furrowed zones. Length: width of pygidium approximately $\frac{2}{3}$ – $\frac{3}{4}$.

Remarks. Although restricted to the variety α , *vulgaris* of Salter, there remains considerable variation within the species. This is mostly accounted for by changes taking place during the ontogeny. These changes may be summarized as follows. The glabella becomes apparently more parallel-sided; the frontal lobe slightly more convex; the furrows straighter; the strong posterior median deflections of the younger stages of both 3S and 2S gradually disappear; 1S becomes more transverse, less deep and less wide. In the pygidium 5 (6) pleurae are recognized in young holaspides; 6 (7) in large adults; a ninth axial segment may sometimes be discerned in large individuals. While in young and juvenile holaspid stages the border of the pygidium is merely an unfurrowed continuation of the pleural zone, the two become separated in adults with a cephalic length in excess of 7.50 mm. by a flattening or shallow furrow. Finally, and of importance phylogenetically, is the presence of short genal mucronations in very young holaspides with a cephalic length of up to 4.40 mm. Six specimens ranging in cephalic length between 2.72 and 4.40 mm. have been observed to possess these characters. The

mucronations are short and stout and are thrown off from the genal angle in a similar manner to the genal spines of *Acastella prima* Tomczykowa and *A. spinosa* (Salter) (text-fig. 3). They are not continuations of the cephalic outline as in the Dalmanitinae. Specimens with cephalic lengths within the range 4.50–7.50 mm. have very acutely angled genae with points in place of projections (text-fig. 3c), i.e. 'a tubercle only in



TEXT-FIG. 3. The development of the genal angle in *Acaste downingiae* (Murchison), compared to the genal condition of *Acastella prima* Tomczykowa and *Acastella spinosa* (Salter). *a*, Small holaspid of *Acaste downingiae* (cephalic length 3.2 mm.) showing genal projections; UN T5034. $\times 4$. *b*, Small holaspid of *A. downingiae* (cephalic length 4.3 mm.) SM A28744. $\times 4$. *c*, *A. downingiae*, juvenile holaspid, projection resorbed but genae remaining distinctly angled (cephalic length 8.8 mm.); NMW G.391.2. $\times 4$. *d*, *Acastella prima* Tomczykowa. Drawing after Tomczykowa 1962a (text-fig. 1c, p. 262). $\times 4$. *e*, *Acastella spinosa* (Salter), holotype, GSM 19412. $\times 4$.

place of a spine' (Salter 1864, p. 25). The specimen figured by R. and E. Richter (1954, pl. 3, fig. 39a) shows this stage in the development of its genal angles. Specimens with cephalic lengths greater than 7.50 mm. have less acutely angled genae, 'rounded off' (Salter, op. cit., p. 25), but still clearly show the positions from which the original projections were resorbed.

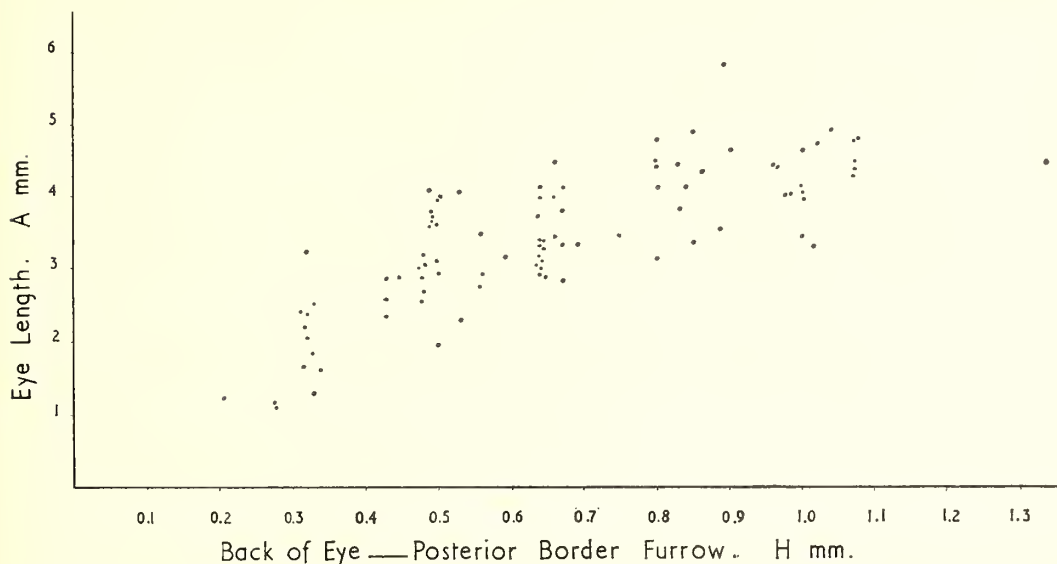
Apart from ontogenetic changes, further variation is observed in *Acaste downingiae*. Rarely, specimens are encountered in which 2S actually reaches and joins with the axial furrows in the adult stages. Equally rare are specimens in which not only 2S but also 1S fails abaxially to reach the axial furrow.

When values of A and H are plotted for 93 specimens of *A. downingiae*, the points are found to fall into five distinct groupings lying on a gentle curve (text-fig. 4). The possibility of a sixth is indicated by the solitary point at the extreme end of the graph. These groupings are interpreted as instars. Each group overlaps the preceding in values of eye length. Further, within each group, with the exception of the first, there appears to be a division into two fields, which is tentatively suggested as being the result of dimorphism.

Relationships. The relationships of *A. downingiae* (Murchison) to *A. inflata* (Salter) are dealt with under comments on the latter. R. and E. Richter (1954, p. 17) have made comparisons with their species, *A. dayiana*. The convexity and degree of tapering of the glabella and the number and distribution of the facets of the visual surface serve to differentiate the two species. No details of the ontogeny of *A. dayiana* are given. R. and E. Richter (1954, pl. 4, figs. 52–56) show, however, that when preserved with the shell,

the border of the pygidium and the furrowed pleural area are continuous, but in the internal mould a flattening separates the two areas.

As mentioned above, the adult of *Acastella prima* Tomczykowa possesses the mucronate projections characteristic of the smallest preserved holaspis stage of *A. downingiae* (text-fig. 3). The close relationships of the genus *Acastella* to members of the Acastinae



TEXT-FIG. 4. The eye length plotted against the distance of the eye from the posterior border furrow for 93 specimens of *Acaste downingiae* (Murchison). The graph shows groupings into five instars, with the possibility of a sixth.

are demonstrated further by Tomczykowa (1962*b*, p. 202) who derives *Scotiella* from it during the Upper Silurian, both genera occurring together in the Rzepin Beds (Upper Ludlow).

H. Hollard (1963, pp. 21–22, text-fig. 1*a–c*) has recently described, from the internal moulds of two pygidia, *Acaste talebensis*, a species of *Acaste* found near the junction of the *Monograptus uniformis* and *M. hercynicus* zones in Morocco. Both pleurae and axis of this species are more strongly convex (tr.) than the condition shown by *A. downingiae*. As a result the pleurae curve more sharply to the posterior. The interpleural furrows are more deeply incised than those shown on the internal moulds of *A. downingiae* and there are traces of segmentation, shown by slight swellings, on the border. The axial termination ends more abruptly and closer to the posterior margin. The two species share a similar outline and segmentation.

Range and Distribution. *Acaste downingiae* (Murchison) s.s. appears to be confined to the Wenlock Limestone of the Welsh Borderlands and West Midlands. Though it occurs typically in a calcareous environment, specimens similar to *A. downingiae*, from the Buckover Section, near Tortworth, Gloucestershire (Curtis and Cave 1964) occur in purplish-red and brownish weathering siltstones and yellow-brown fine-grained calcareous sandstone. Again, forms similar to *A. downingiae* occur in the grey-green calcareous siltstones of the highest Black Cock Beds (Lower Bringewood Beds) in the Golden

Grove, Llandeilo, and may even pass into the lowest Middle Bringewood Beds in the Llandovery area (J. F. Potter, personal communication). At Freshwater East, Pembs., *A. downingiae* is replaced by *A. subcaudata* (Murchison). The species has not been recorded from the Pen-y-lan inlier.

A. downingiae s.s. is definitely recorded from the following localities; Walsall, Staffs.; Dudley (Wren's Nest and Castle Hill), Worcs.; Benthall Edge, Salop; Wenlock Edge, Salop (rare); Malvern, Worcs.; Ledbury, Herefordshire.

Acaste inflata (Salter 1864)

Plate 29, figs. 9-16

1864 *Phacops (Acaste) Downingiae* Murchison, var. γ , *inflatus* Salter, p. 27, pl. 2, fig. 30 (OUM C9), not figs. 31 (GSM 19305), 32 (GSM 19314) or 33 (GSM 19306).

Lectotype (here designated). Salter 1864, pl. 2, fig. 30; OUM C9, figured here, pl. 29, figs. 9-14. Wenlock Limestone, Ledbury Railway Tunnel, Ledbury, Herefordshire.

Diagnosis. A species of *Acaste* characterized by its strongly convex (sag.) frontal lobe and by the high convexity (tr.) of 1L which causes it to slope abaxially well below the level of 2L; 2L and 3L are also more convex (tr. and sag.) than in *A. downingiae*, the convexity of the lobes causing the furrows to appear more closely spaced than in that species. Visual surface at maximum height with rows of 7 lenses alternating with 6. Pygidium with 7-8 axial segments, 5 pleural segments.

Description. Cephalon subtriangular in outline. Narrow, triangular area of librigena prominently projecting in front of glabella. Surface of test finely granular. Length of cephalon approximately $\frac{1}{2}$ - $\frac{2}{3}$ width.

Glabellar plan as in *A. downingiae*. Axial furrows gently curving round 2L and 3L. Frontal lobe rounded both anteriorly and antero-laterally, moderately to strongly convex (tr. and sag.). 2L and 3L abaxially fused, roughly equal in size, with slightly less convexity (tr.) than frontal lobe. 1L about half as wide (exsag.) as 2L, with much stronger convexity (tr.) than 2L in posterior profile, sloping abaxially well below the dorsal level of 2L. Side furrows 3S long, shallow, fairly wide, curving backwards with posterior median deflection. 2S shorter than 3S, impressed to similar depth, transverse, abaxially linear, medianly with marked deflection to posterior; failing laterally to join with axial furrows. 1S of similar length to 2S, wider and deeper, deflected both abaxially and medianly to anterior. Short sagittal furrow between median extremities of 3S. Side furrows appear closer together than in *A. downingiae* due to the greater convexity of the lobes (the 'crowded' condition of Salter 1864, p. 27).

Occipital furrow abaxially a little deeper than 1S, becoming shallow but still well defined sagittally. Occipital ring narrow (sag.), as wide (tr.) as 1L and with similar convexity (tr.); in lateral profile raised higher above the side lobes than in *A. downingiae*.

Genae strongly sloping to narrow flattened border. Preglabellar furrow shallow, very narrow (sag.). Postocular section of facial suture cutting lateral cephalic margin opposite middle of 2L; preocular section dorsal intramarginal, becoming marginal at antero-lateral edges of frontal lobe. Fixigenae postero-laterally angled in adults; with deep but narrow (exsag.) posterior border furrow.

Eye crescentic in plan, rather small; situated centrally between cephalic margin and

glabella, on high ocular platform which falls steeply to antero-lateral and lateral margins of cephalon. In lateral profile top of eye sloping gently to anterior; in anterior profile, well below level of glabellar surface. Eye extending from posterior margin of 1L to anterior margin of 3L; closer to posterior border furrow than in *A. downingiae*; H/A, 5–18 per cent.; A/G, 47–56 per cent.; A/Gn, 40–48 per cent. Palpebral lobes high; palpebral areas relatively wide, with low inclination to axial furrows.

Visual surface overhanging ocular platform; gently convex outwards. Up to 130 closely packed lenses arranged in roughly alternating vertical columns containing at maximum height 6 or 7 individual lenses, with a typical diameter of up to 0.2 mm. and rounded or polygonal in outline. Interspaces with similar texture to surrounding genae.

Pygidium subtriangular in outline, margin entire; in posterior profile slightly vaulted. Axis raised above axial furrows and pleurae; moderately to strongly convex; composed of 7–8 segments and a rounded, unsegmented terminal piece, tapering gradually to posterior; segments 1–3 well defined. Pleurae moderately convex; 5 in number. Pleural furrows strongly impressed, interpleural furrows weak. Border wide, as in adult *A. downingiae*, with a pronounced flattening separating the segmented and unsegmented pleural areas. Length of pygidium $\frac{2}{3}$ – $\frac{4}{5}$ width.

Comments on figured material. All the specimens used by Salter were derived from the Malvern–Ledbury area. His fig. 30 was obtained by Dr. R. B. Grindrod from the Ledbury railway tunnel. Figs. 31 and 32 were merely stated in 1864 to be from Ledbury, no stratigraphic horizon being given. In 1853, however, Salter (p. 9) recorded the same specimens from ‘the Wenlock limestones of the Malverns’ and from ‘the Wenlock Limestone, Ledbury’ respectively. Fig. 33 is said to be from Eastnor, near Ledbury.

In the text (1864, p. 27), it is implied that only fig. 30 represents the variety with any certainty. The diagnosis is given from this specimen as follows: ‘The glabella is greatly swollen, so as to be very convex, instead of flattened, in front. All the furrows are indeed distinct and in their proper situations, but from the inflation of the glabella they appear crowded. The eyes are small.’ Accordingly this specimen is here selected as lectotype for the species.

Of the other specimens figured Salter appears to have been less certain. Fig. 31, he states, ‘probably . . . belongs to var. β ’. This specimen has a similar furrow pattern to *A. inflata* but differs from it in the rather depressed frontal lobe more typical of *A. downingiae*: the low convexity of the glabellar lobes; the width (trans.) and convexity of the occipital ring and its failure to rise, in lateral profile, significantly above the glabellar side lobes. As such its characteristics are more compatible with *A. downingiae*, with which it is here included.

Fig. 32 is a cephalon of exceptional size (occipital glabellar length 20 mm., cephalic width 32 mm.). The eyes are missing. Although the frontal lobe is strongly convex (sag.), the side lobes lack the convexity typical of *A. inflata*. Furthermore, side furrows 3S and 2S are relatively shorter and the transverse convexity of 1L and the occipital ring are not nearly so pronounced as in that species. No other specimens referable to *A. inflata* approach anywhere near this specimen in size. Large specimens of *A. downingiae* have, however, been observed from the Ledbury area and of *Acastocephala macrops* from Pen-y-lan quarry, Cardiff. Due to its highly convex frontal lobe and deep side furrows this specimen has been refigured here with the latter species.

Fig. 33, a large pygidium (length 11 mm., width 15 mm.), is here certainly referred to the *downingiae* group. It has in common with that species 8 axial segments, 5 pleural segments, and the typical convexity when viewed in posterior profile. It is also wider than the typical pygidium of *A. inflata*.

Relationships. *A. inflata* appears to be closely related to *A. dayiana* R. and E. Richter from the Köbbinghauser Dayia-Schichten (see R. and E. Richter 1954, pp. 14–16, pl. 4, figs. 45–56). The frontal lobe of their species has a slightly greater convexity (sag.), and there is a higher degree of tapering of the glabella. The general glabellar plan and convexity of the lobes is very similar. At its maximum height the visual surface of *A. dayiana* carries rows of 5 lenses alternating with 6, and the total number of lenses borne by the surface is only 94. Although the two species have essentially similar cephalic outlines, the pygidium of *A. dayiana* is more subsemicircular than subtriangular in outline and is also apparently wider.

A. inflata is well differentiated from *A. downingiae* (Murchison) by virtue of its highly convex glabellar lobation. The visual surface of *inflata* carries 6 lenses alternating with 7, while that of *downingiae* has 8 alternating with 9. The eye of *inflata* is also a little closer to the posterior border furrow, H/A, 5–18 per cent. compared with 12–30 per cent. for *downingiae* (see text-fig. 2). Both cephalon and pygidium of *inflata* are slightly narrower than those of *downingiae*, the ranges of length/width for the cephalae being 51–68 per cent. and 46–62 per cent. respectively and for the pygidia, 65–85 per cent. and 60–80 per cent. In general it may be said that the pygidia are too closely related to be differentiated further. Compared with *downingiae*, the sample of *inflata* studied is small and the detailed ontogenetic changes have not been set out as for the former as the smallest holaspis stages have not yet been seen.

Range and Distribution. From the available material *Acaste inflata* appears to be confined, like *Acaste downingiae*, to the Wenlock Limestone of the Welsh Borderlands and West Midlands. Specimens close to *A. inflata*, however, occur in the siltstones and calcareous sandstones of the Buckover Section, near Tortworth, Gloucestershire (Curtis and Cave 1964). A further similar species with strongly convex glabellar lobes has been collected by the author from Lower Elton Beds outcropping near Upper Millichope, Shropshire.

The species has been identified with certainty from the following localities: Dudley (Wren's Nest), Worcs.; Malvern (railway tunnel), Worcs.; Ledbury (railway tunnel), Herefordshire.

Additional Material. *A. inflata* is not a common trilobite. The writer has seen to date but 19 specimens, the bulk of which are to be found in the Grindrod Collection, Oxford University Museum.

From the Wenlock Limestone of Ledbury; OUM C 559; specimens undocumented but probably also from this locality and horizon; OUM C597, C610, C612–20. From the Wenlock Limestone, Malvern; GSM 19301–3. From the Wenlock Limestone of Dudley; BM In36154, In36156; NMW 27.110.G.998.3.

Acaste subcaudata (Murchison 1839)

Plate 30, figs. 1–16

1839 *Asaphus subcaudatus* (n.s.) Murchison, p. 655, pl. 7, fig. 10.

1839 *Asaphus Cawdori* (n.s.) Murchison, p. 655, pl. 7, fig. 9.

1848 *Phacops Downingiae* Murchison; Salter, p. 336, pl. 5, figs. 2 (untraced), 3 (GSM 19377) and 4 (untraced).

1853 *Phacops Downingiae* Murchison; Salter, p. 1 (both *Asaphus Cawdori* and *A. subcaudatus* classed as junior synonyms of *P. Downingiae*).

1921 *Phacops Downingiae* (Murchison); Dixon, p. 21, footnote 6.

Holotype. Murchison 1839, pl. 7, fig. 10; GSC 6591. The holotype is 'possibly from the Wenlock Series' (Dixon 1921, p. 21), Freshwater East, Pembrokeshire.

Diagnosis. A species of *Acaste* with frontal lobe more strongly convex (sag.) than that of *A. downingiae* but less so than *A. inflata*; 3S more faintly impressed than in *A. downingiae*. Fixigenae of young holaspides with postero-lateral projections, resorbed in later moults, as in *A. downingiae*. Eyes small; visual surface narrow, similar to *A. dayiana*, with fewer lenses than *A. downingiae*, bearing at the maximum height rows of 5 lenses alternating with 6. Pygidium rather long; 7 (8) axial segments; 5 (6) pleurae; more strongly convex (tr.) than *A. downingiae*; border narrow, separated by marked flattening from furrowed pleural area at all holaspid stages. Margin entire throughout holaspid ontogeny.

Description (based on internal moulds). Cephalic outline subtriangular to ogival as in *A. downingiae*. The narrow, triangular area of librigena anterior to the frontal lobe which is common to other species of *Acaste* is also present in *A. subcaudata*.

Glabella anteriorly rounded, laterally more or less subparallel-sided, transverse width decreasing evenly to posterior. Axial furrows linear, without the gentle curve round 2L and 3L which characterizes *A. downingiae*, diverging at a slightly greater rate than *A. downingiae* in small specimens, appreciably less in large individuals. Frontal lobe anteriorly rounded, antero-laterally more parallel-sided than in *A. downingiae*. In lateral profile frontal lobe has a moderate convexity (sag.) which is greater than that of *A. downingiae* but less than *A. inflata*. Small individuals have a sagittal convexity similar to or greater than the adult of *A. downingiae*. 2L and 3L of roughly equal size, abaxially fused. 1L about half as wide as 2L; in young holaspides transverse convexity of 1L is slightly greater than that of 2L but in adults is less apparently so. 3S sigmoidal, long, more faintly impressed on the internal mould than in specimens of *A. downingiae* preserved with the shell, with a distinct median deflection to the posterior which appears to be present at all holaspid ontogenetic stages. 2S shorter than 3S, impressed to a similar depth, linear, transverse or with very faint posterior median deflection in some individuals; failing laterally to reach the axial furrows. 1S much wider and deeper but also shorter than 2S or 3S, curving both medianly and abaxially to the anterior.

Occipital furrow as wide and deep abaxially as 1S. Occipital ring narrow (sag.), with similar transverse width and convexity to 1L; in lateral profile barely rising above the level of the glabellar side lobes.

Fixigenae in young holaspides produced postero-laterally into short, stout projections which appear to be longer than in specimens of *A. downingiae* of corresponding size. In larger specimens the projection is resorbed but there remains a distinct point. Genal projections have been observed in specimens with a cephalic length of up to 2.9 mm. but a full range of sizes has yet to be collected. Adult genae are completely unknown, but those of intermediate stages are distinctly angled.

Eyes rather small, similar in plan to those of *A. inflata*, situated centrally on the genae on low ocular platform, as in *A. downingiae*; extending roughly from 1S to confluence of 3S and axial furrows; A/G, 45–63 per cent.; A/Gn, 37–46 per cent. In lateral profile the top of the eye slopes gently to the anterior and fails to reach the level of the glabella surface. Palpebral areas with low inclination to axial furrows. Fixigenal area between

back of eye and posterior border furrow similar in extent to *A. downingiae*, H/A, 12–27 per cent.

Visual surface known only from one juvenile specimen; rather narrow bearing fewer lenses than in *A. downingiae*, at the maximum height of the surface arranged in alternating columns of 5 or 6 (as in *A. dayiana*).

Outline of hypostome subrectangular; anterior margin rounded and antero-laterally produced into short wings; lateral margins very gently curved abaxially; posterior margin gently curved backwards; postero-lateral corners truncate, curved. Posterior border narrow, separated from median body by wide, well-defined furrow; lateral borders extremely narrow. Median body moderately convex adventrally. Maculae situated halfway along body, close to lateral borders.

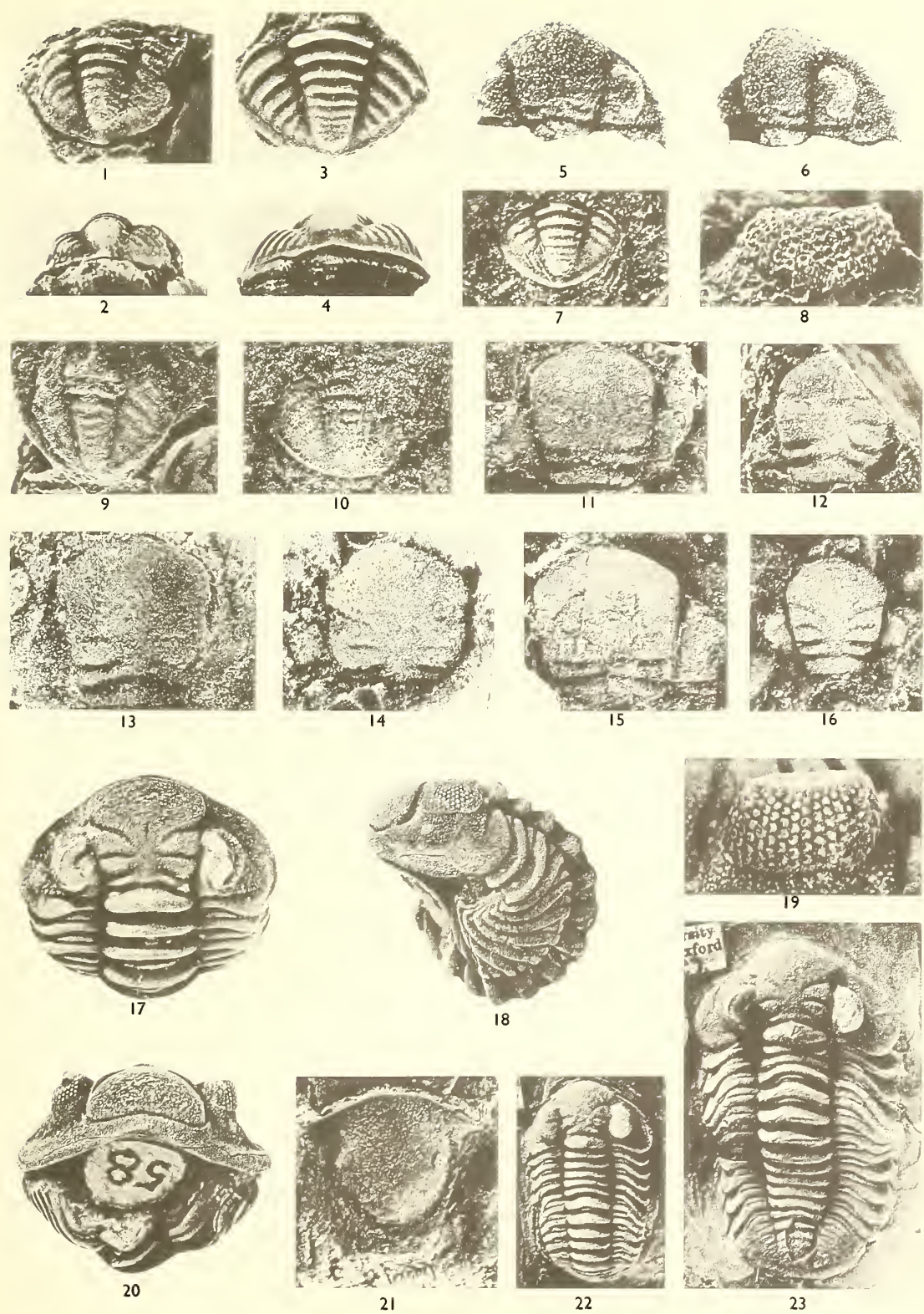
Pygidium subtriangular in outline; in posterior profile rather strongly convex (tr.). Axis strongly convex (tr.), raised well above axial furrows and pleurae; typically with 7 (8) segments, the eighth being discernible only in cases of exceptional preservation; narrow postaxial border; axial segments 1–3 are most distinct, separated by well-defined transverse furrows; succeeding segments rather poorly defined towards the posterior. Pleurae generally more strongly convex (tr.) than in *A. downingiae*, falling off rapidly in postero-lateral direction; 5 (6) in number. Pleural furrows strongly defined, wide and deep; interpleural furrows, with the exception of the first, rarely preserved on internal moulds. Border narrow, separated from furrowed pleural area by a marked flattening at all holaspisid growth stages. Margin entire throughout holaspisid ontogeny.

Type Material. Specimens, GSC 6591 and 6592 are labelled as having been used by Murchison (1839) for his illustrations of *Asaphus subcaudatus* and *A. cawdori*. GSC 6591 is here selected as the holotype

EXPLANATION OF PLATE 30

Figs. 1–16. *Acaste subcaudata* (Murchison 1839). 1–2. GSC 6591; Holotype; figured Murchison 1839, pl. 7, fig. 10. Probably Wenlock Series, Freshwater East, Pembrokeshire. 1, Dorsal view, internal mould of pygidium, $\times 3$. 2, View from posterior, $\times 3$. 3–4. GSM 19377; figured Salter 1848, pl. 5, fig. 3. Probably Ludlow Series, Freshwater East, Pembrokeshire. 3, Dorsal view, internal mould of pygidium, $\times 3$. 4, View from posterior, $\times 3$. 5–6. GSM 102597; Ludlow Series, Freshwater East, Pembrokeshire. 5, Internal mould of young holaspisid cephalon with genal projection, $\times 4$. 6, Oblique view, $\times 4$. 7. GSM 102605; Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of pygidium, $\times 3$. 8. GSM 102604; Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of eye, $\times 8$. 9. GSC 6592; figured Murchison 1839, pl. 7, fig. 9 as *Asaphus cawdori*. Probably Wenlock Series, Freshwater East, Pembrokeshire. Internal mould of pygidium, $\times 3$. 10. GSM 102603; Ludlow Series, Freshwater East, Pembrokeshire. Latex cast from internal mould of pygidium, $\times 3$. 11. GSM 102602; Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of cranium, $\times 3$. 12. GSM 102606; Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of glabella, $\times 3$. 13–14. GSM 102600–1; Ludlow Series, Freshwater East, Pembrokeshire. 13, Internal mould of cranium, $\times 3$. 14, Latex cast from external mould showing side furrows 2S and 3S more deeply incised, $\times 3$. 15. GSM 102599, Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of cranium, $\times 3$. 16. GSM 102598; Ludlow Series, Freshwater East, Pembrokeshire. Latex cast from external mould of cranium, $\times 3$.

Figs. 17–23. *Acastoides constricta* (Salter 1864). 17–20. BU 58; figured Salter 1864, pl. 2, fig. 15a–c. Wenlock Limestone, Dudley, Worcs. 17, Dorsal view of cephalon, $\times 3$. 18, Lateral view, $\times 3$. 19, Eye, $\times 8$. 20, View from anterior, $\times 3$. 21. BM 58897; Wenlock Limestone, Dudley, Worcs. Hypostome, $\times 6$. 22. OUM C8; figured Salter 1864, pl. 2, fig. 14. Wenlock Shale, Malvern Tunnel, Worcs. Dorsal view, $\times 2$. 23. OUM C7; Lectotype; figured Salter 1864, pl. 2, fig. 13, 13a. Wenlock Shale, Malvern Tunnel, Malvern, Worcs. Dorsal view, $\times 2$.



for *Acaste subcaudata* (Murchison). In its segmentation, its degree of convexity and in the nature of its border, it is indistinguishable from the specimen (GSM 19377) figured by Salter (1848, pl. 5, fig. 3) and from others collected by the author from Freshwater East. GSC 6592, the holotype of *Asaphus cawdori*, is a specimen most difficult to evaluate, largely due to its distortion and indifferent preservation. There is also difficulty in equating it with Murchison's figures. Murchison (1839, pl. 7, fig. 9) originally figured a block showing two small pygidia but in 1872 (pl. 18, fig. 3) only one pygidium is depicted. In both illustrations the specimens are complete and undistorted. GSC 6592, therefore, can only doubtfully be identified with *A. cawdori*. Essentially similar to *Acaste subcaudata* in construction it is here included with reserve in the synonymy of that species. Stubblefield (1938, p. 31) states that Salter's fig. 2 (pl. 5) has been possibly compounded from two specimens in the Geological Survey Collections, GSM 19376 and 19378, both being incomplete cranidia and neither showing the full outline or extent of the cephalon as depicted by Salter. The specimen used for fig. 3 is thought to be GSM 19377. That used for fig. 4 is untraced.

Relationships. *A. subcaudata* differs from *A. downingiae*, to which it is closely related, by its more convex (sag.) frontal lobe; by the tapering of the glabella; the depth of impression of the side furrows, which would normally be expected to be deeper on the internal mould (the furrows must be quite faint on the shell); the number of facets of the eye and their distribution; the general shape of the hypostome and the convexity and segmentation of the pygidium.

From *A. inflata*, *A. subcaudata* differs by the lower convexity (sag.) of the frontal lobe; the lower convexity (tr.) of the preoccipital glabellar lobe; by the number and distribution of eye facets and by the same pygidial characters as stated above for *A. downingiae*.

A. dayiana has a more strongly convex (sag.) frontal lobe and a greater degree of glabellar tapering. The convexity (tr.) of the side lobes would also appear to be stronger. Pygidial segmentation and the presence of a border flattening on the internal moulds are common to both species, as is the content of the visual surface. A common environmental control may account for these similarities.

Range and Distribution. *A. subcaudata* is at present only known from strata occurring at Freshwater East, Pembrokeshire, attributed by Dixon (1921) to the Wenlock and Ludlow Series. GSM 102597–606 were collected by the author from the Ludlow Series of the South side of Freshwater East Bay, from rottenstone bands in group (4) of Dixon (1921, p. 14). These beds are accessible where the High Water Mark shown on Dixon's sketch map (1921, p. 23) is marked as meeting the cliff. Approximate Grid Ref., SS 0168/9739.

Additional Material: GSM 19376–8, 102597–606.

Genus *ACASTOIDES* Delo 1935 *Acastoides constricta* (Salter 1864)

Plate 30, figs. 17–23

- 1864 *Phacops (Acaste) Downingiae* Murchison, variety or subspecies ϵ , *constrictus*. *Phacops constrictus*. Salter, pp. 27–28, pl. 2, figs. 13 (OUM C7), 14 (OUM C8), 15 (BU 58).
1954 *Acaste (Acastoides) constricta* (Salter 1864). R. and E. Richter, pp. 17–18, pl. 3, figs. 42, 43.
1965 *Acastoides constricta* (Salter 1864); Clarkson, p. 22, pl. 3, figs. 10–12.

Lectotype (here designated). Salter 1864, pl. 2, fig. 13; OUM C7. Wenlock Shale, Malvern Tunnel Malvern, Worcs.

Remarks. R. and E. Richter (1954, pp. 17–18) have given an account of this species but have omitted to consider the hypostome. Accordingly no detailed description will be given here. Instead, an extended diagnosis is given together with an account of the hypostome and notes on the relationship of *Acastoides constricta* with other species of the genus.

Extended diagnosis. A species of *Acastoides* characterized by a strongly convex (sag.) frontal lobe which frequently extends to the anterior margin of the cephalon; 1L with a greater transverse convexity than 2L, sloping abaxially below the level of 2L; 3S shallow, wide, sigmoidal, with strong posterior median deflection; 2S long, transverse, just reaching the axial furrow; 1S and 3S tending to converge adaxially. Occipital ring raised high above level of glabella, with axial node. Genae postero-laterally rounded off. Preocular section of facial suture marginal or just dorsal intramarginal. Eyes small, close to glabella, extending from occipital furrow to anterior edge of 3L, raised on high ocular platform nearly to the level of the glabella. Palpebral lobes high; palpebral areas narrow, with high inclination to the axial furrows. Visual surface with 104+ lenses, at maximum height bearing columns of 6 alternating with 7. Pygidium subsemicircular in outline, posteriorly truncate, scarcely vaulted in posterior profile; margin entire. Axis short, with low convexity (trans.), composed of 5 (6) segments and wide axial terminal piece. Pleurae weakly convex (trans.), 4 in number; furrows weakly impressed, pleural furrows being slightly stronger than interpleural furrows. Border flat and broad.

Hypostome outline subquadrate; anterior margin arcuate, antero-laterally extended into short wings; lateral margins curving very gently abaxially; posterior margin short, gently curved backwards; postero-lateral margins truncate. Lateral borders narrow; posterior border wide (sag.). Median body strongly convex adventrally, without trace of median furrow. Maculae large, ovoid and prominent, situated on lateral margins of median body just inside the anterior half of the structure. Surface coarsely granular.

The hypostome of *A. constricta* (Salter) differs from that of *Acaste downingiae* in its more highly convex median body with prominent maculae; in the arcuate outline of the anterior margin and the wide (sag.) posterior border. Though similar in structure to the hypostome of *Acastocephala macrops* (Salter), that of *Acastoides constricta* contrasts strongly by its distinctive coarse ornament.

Relationships. In construction the cephalon of *Acastoides constricta* appears to be closely related to *A. heuni heuni* R. and E. Richter 1952 described from the Wiltzer Schichten, Upper Emsian. *A. constricta* may be differentiated by its more marginal frontal lobe; greater degree of glabellar tapering; eyes larger and more extensive; visual surface with a greater number of lenses and a maximum of 7 in any column compared with 4 in *A. heuni heuni*; the pygidial margin is entire and non-denticulate.

A. constricta is similarly distinct from *A. heuni posthuma* R. and E. Richter 1952 from the Heisdorfer Schichten, high Upper Emsian, and from *A. paeckehuanni* R. and E. Richter 1939, from the Pendik Schichten, Pendik, Bosphorus, high Upper Emsian in age.

Range and Distribution. *Acastoides constricta* is recorded from the Wenlock Shale and Wenlock Limestone of Dudley, Walsall and the Malvern Tunnel, Malvern, Worcs. It appears to be restricted to the Wenlockian of the Welsh Borderlands.

Additional Material. In addition to the lectotype and paratypes the following material has been located.

From the Wenlock Shale of the Malvern Railway Tunnel: OUM C561–7, C576, C609, C611; BM 59040, 59048; GSM 19242–3. From the Wenlock Limestone, Malvern; BM 44251; GSM 19304; labelled Wenlock? Limestone, Malvern; BM 58897, 59048; labelled simply Malvern; GSM 49836. From the Wenlock Limestone, Walsall; GSM 22450. Unlocalized specimen; GSM 49838.

Family DALMANITIDAE Vogdes 1890

Subfamily ACASTAVINAE Struve 1958

ACASTOCEPHALA gen. nov.

Derivation of name. Trilobites with cephalon constructed in a similar manner to that of *Acaste* Goldfuss.

Type species. *Acastocephala macrops* (Salter 1864).

Other species. *Acastocephala dudleyensis* sp. nov.

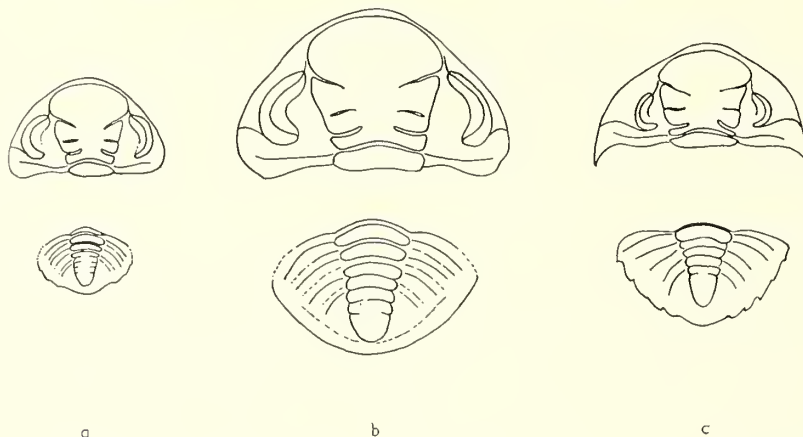
Diagnosis. Cephalon typically acastid in construction but with larger eye; visual surface containing, at maximum height, rows of 10 lenses in *A. macrops* (Salter), 9 in *A. dudleyensis* sp. nov. Pygidium wide, weakly furrowed; 4–5 pleural segments; 7 axial segments. During ontogeny of both known species smallest holaspides have a denticulate lateral pygidial margin; denticulations resorbed in succeeding growth stages to give adult with typically entire margin.

Range and Distribution. Wenlock Shale, Malvern, Worcs; ? Wenlock Shale, Pen-y-lan, near Cardiff; Wenlock Limestone, Malvern and Dudley, Worcs.

Relationships. *Acastocephala* differs from *Acaste* Goldfuss in the following characteristics. The eye is larger, carries a greater number of facets and is relatively closer to the posterior border furrow. The pygidium has a lower convexity (tr.) and is more poorly segmented. Both pleural and interpleural furrows are weaker. As in *Acaste*, the fixigenae of the smallest holaspides are provided postero-laterally with short projections but these are not nearly so long or distinct and appear to be more rapidly resorbed. In addition, young holaspides of *Acastocephala* have a denticulate lateral pygidial margin which contrasts with the entire margin of the adults, while the margin of *Acaste* is entire in holaspides of all sizes. Posteriorly the margin is without trace of a caudal projection. The hypostome is larger and more convex (tr. and sag.) than in *Acaste* and the maculae are larger and more clearly defined.

Though closely related to *Acaste*, *Acastocephala* is equally close to *Acastava* R. and E. Richter 1954. The glabellae are essentially similar in construction. Schmidt's text-figure of *Acastava atava* (1907, p. 10) shows side furrows 3S to be obliquely directed, without a posterior median deflection and very similar to the condition of *Acastocephala macrops*. Similarly, 2S is linear, transverse and only just failing abaxially to reach the axial furrows. In *Acastava atava* the eyes are large but the visual surface at its maximum height contains columns with only 6 lenses. *A. atava* also differs in retaining genal spines into adult holaspide stages. When preserved with the shell the pygidial margin of *A. atava* is entire but the internal mould possesses 5 pairs of lateral denticulations (see Schmidt 1907, p. 10, text-fig. 1 and R. and E. Richter 1954, pl. 6, figs. 81 and 82) formed in exactly the same manner as those produced in young holaspides of *Acastocephala* (text-fig. 5). Pygidial

segmentation is also similar. *Acastava? schmidtii* (R. Richter), like *Acastocephala dudleyensis*, possesses large eyes situated both close to the glabella and to the posterior border furrow. *Acastocephala* is confined, in the British Isles, to the Wenlockian while *Acastava* ranges in the Lower Devonian from Siegenian to Emsian. The affinities between these two genera may prove to be significant phylogenetically.



TEXT-FIG. 5. A comparison of *Acastocephala macrops* (Salter) and *Acastava atava* (W. E. Schmidt). a, Young holaspid of *A. macrops* showing lateral denticulations on pygidial margin of shell; BU 862. $\times 2\frac{2}{3}$. b, Adult of *A. macrops* showing entire pygidial margin; BU 861. $\times 2$. c, Adult of *Acastava atava* showing denticulations along lateral pygidial margin on the internal mould. Drawing after Struve 1959, p. O476, fig. 377, 1a, 1b. $\times 2\frac{2}{3}$.

Acastocephala is quite distinct from *Acastella* Reed 1925. *Acastella* is characterized by slender genal spines and by a caudal mucronation throughout its ontogeny. Pygidial segmentation and the size and position of the eyes in *Acastella* are essentially similar to *Acaste*. Some species of *Acastella* have a smooth pygidial margin when preserved with the shell or as internal moulds as, for example, in *A. heberti heberti* (Gossellet), *A. patula* Hollard, and *A. jacquemonti* Hollard. Others, *A. tiro* R. and E. Richter and *A. heberti elsana* R. and E. Richter, produce lateral denticulations on the internal mould but not on the shell.

The genus *Acastoides* Delo 1935, is characterized by a subpentangular cephalic outline and eyes set high up on the genae. The shape, convexity and segmentation of the pygidium differ considerably from *Acastocephala*. In some species, *Acastoides henni henni* (R. Richter) and *A. paeckelmanni* R. and E. Richter, there is a tendency to develop spine-like denticulations along the pygidial margin but they differ from those of *Acastella*, *Acastava*, and *Acastocephala* in that they are directed ventrally. *Acastoides constricta* (Salter) and *Acastocephala macrops* (Salter) occur together in the Wenlock Shale of Malvern.

The decision to erect a new genus to cover trilobites referred to Salter's variety *macrops* is based largely on the differences of these species from both *Acaste* and *Acastava*. The larger number of eye facets and the lack of genal spines in the adult prevent inclusion of these trilobites in the genus *Acastava*, while the pygidial margins of the young and

weaker pygidial furrowing preclude their inclusion in the genus *Acaste*. A further consideration has been the possibility of a phylogenetic link between *Acastocephala* and *Acastava*.

Acastocephala macrops (Salter 1864)

Plate 31, figs. 1–15, Plate 32, figs. 1–2

1864 *Phacops (Acaste) Downingiae* Murchison, var. β , *macrops*, Salter, pp. 26–27, pl. 2, figs. 27 (BU 861), 29 (GSM 19319), 32 (GSM 19314), *not* figs. 26 and 28 (specimens untraced).

Lectotype (*here designated*). Salter, 1864, pl. 2, fig. 27; BU 861. Wenlock Shale, Malvern, Worcs.

Diagnosis. A species of *Acastocephala* gen. nov., with moderately convex (sag.) frontal lobe; 3S wide and deep, opening out abaxially, 2S short, linear, sloping gently abaxially to posterior. Eyes large, situated centrally on the genae; extending anteriorly past the confluence of 3S and the axial furrows. Visual surface at maximum height bearing 9 lenses alternating with 10. Pygidium with low convexity; 4 (5) pleurae, 7 axial segments. Border undifferentiated from furrowed pleural area. Margin in small holaspides denticulate, entire in adults.

Description. Cephalic outline ogival, subtriangular or in large individuals, more rarely, subsemicircular. In common with species of *Acaste* and *Acastella* there projects, anterior to the glabella, a narrow triangular area of librigena, in this species not as extensive as in *Acaste downingiae* or *Acaste inflata*. Surface of test finely granular. Length: width of cephalon $\frac{1}{2}$ – $\frac{2}{3}$.

Glabella anteriorly rounded, laterally subparallel. Angle of divergence of axial furrows similar to *A. downingiae*. Degree of tapering in transverse width rather irregular, giving, in some specimens, a distinctly waisted appearance (cf. the lectotype), which is less apparent in specimens which have either lost the greater part of their shell thickness or are preserved as internal moulds. Frontal lobe both anteriorly and antero-laterally rounded, with moderate to strong convexity (sag.) in young holaspides and adults. 2L and 3L laterally fused, more or less equal in size, slightly less convex (tr.) than the frontal lobe. 1L narrow (exsag.), about half the size of 2L. Convexity (tr.) of 1L insignificantly greater than 2L in specimens with shell but slightly greater in internal moulds. 3S long, sigmoidal, wide and deep, opening out and becoming deeper abaxially; with distinct posterior median deflection in the majority of specimens. 2S shorter, less deep than 3S, linear, transverse, sloping gently to the posterior abaxially, generally failing laterally to join with axial furrows but in some examples very nearly attaining this condition. 1S only a little deeper than 3S, longer than 2S, deflected both medianly and abaxially to anterior.

Occipital furrow impressed to similar depth as 1S. Occipital ring typically a little wider (trans.) than 1L and with similar convexity (tr.). In lateral profile failing to rise significantly above level of glabellar side lobes.

Genae restricted in area due to size and position of eyes. Postocular section of facial suture cutting lateral cephalic margin opposite the posterior edge of 2L; preocular section dorsal intramarginal but may become almost marginal at antero-lateral margins of glabella as in *Acaste inflata*. Genae postero-laterally angled in young holaspides, rounded in adults.

Eyes large, subcrescentic in plan, occupying a large area of the gena, situated a little closer to the cephalic margin than to glabella, especially in young specimens; ocular platform low. In lateral profile top of eye sloping gently to anterior and failing to reach the level of the top of the glabella. Extending from occipital furrow or mid 1L to posterior edge of frontal lobe. Palpebral lobes low but clearly defined; palpebral areas with low inclination to axial furrows. Area of fixigena between back of eye and posterior border furrow narrow; H/A, 6–17 per cent.; A/G, 53–70 per cent.; A/Gn, 45–65 per cent.

Visual surface overhanging slightly the ocular platform, gently convex outwards; sloping more strongly outward-backwards than outward-forwards. Surface bearing a greater number of lenses (in excess of 170) than in species of *Acaste* and *Acastella*. Columns arranged in rows containing at maximum height of surface 9 or 10 lenses. Interspaces non granular.

Hypostome subrectangular in outline; anterior margin rounded, produced antero-laterally into rather long wings, behind which lie shallow notches; posterior margin gently curved to anterior; postero-lateral corners truncated. Lateral borders of undetermined extent; posterior border wide (sag.), bearing a transverse ridge. Median body strongly convex adventrally, with faint median furrow. Maculae large, ovoid tubercles situated laterally and in anterior half of median body. Fine granular ornament overall.

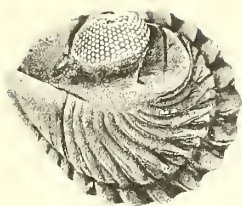
Pygidium subtriangular or subsemicircular in outline; in posterior profile with low convexity (trans.). Axis with low or moderate convexity (tr.), barely raised above axial furrows and pleurae; composed of at least 7 segments of which the anterior 3 are most distinct and separated by well-defined transverse furrows, segmentation becoming less distinct thereafter towards the posterior. Pleurae with low convexity (tr.) in posterior profile; 4 (more rarely 5) in number. Furrows weakly impressed, pleural furrows stronger than interpleural furrows, the latter being well defined only on the first pleura or adaxially on the succeeding pleurae. Border wide, separated both in adults and young by a very shallow flattening, more obvious in the former than the latter and in internal moulds. Margin in young holaspides (with cephalic lengths of up to 5.45 mm. and pygidial lengths up to 4.40 mm.) provided laterally with 3 pairs of short denticulations associated with the first 3 posterior pleural bands. In the adult these denticulations are resorbed to give an entire margin. No trace has been seen at any holaspide stage of a caudal spine or projection.

EXPLANATION OF PLATE 31

Figs. 1–15. *Acastocephala macrops* (Salter 1864). 1–5. BU 861; Lectotype; figured Salter 1864, pl. 2, fig. 27. Wenlock Shale, Malvern, Worcs. 1, Dorsal view of cephalon, $\times 2$. 2, Lateral view, $\times 2$. 3, Dorsal view of pygidium, $\times 2$. 4, Posterior view of pygidium, $\times 2$. 5, Eye, $\times 8$. 6–7. GSM 19314; figured Salter 1853, pl. 1, fig. 14; 1864, pl. 2, fig. 32. Wenlock Limestone, Ledbury, Herefordshire. 6, Lateral view of cephalon, $\times 2$. 7, Dorsal view of cephalon, $\times 2$. 8–9. BM 44319; Wenlock ?Shale, Pen-y-lan, nr. Cardiff. 8, Lateral view of complete specimen, $\times 2$. 9, Dorsal view of cephalo-thorax, $\times 2$. 10. BM 44323; Wenlock ?Shale, Pen-y-lan, nr. Cardiff. Internal mould of pygidium, $\times 2$. 11. GSM 19319; figured Salter 1864, pl. 2, fig. 29. Wenlock ?Shale, Pen-y-lan, nr. Cardiff. Internal mould of cephalo-thorax, $\times 2$. 12–15. BU 862; Wenlock Shale, Malvern, Worcs. Enrolled dorsal exoskeleton of young holaspide. 12, Dorsal view of cephalon, $\times 4$. 13, Lateral view, $\times 4$. 14, Dorsal view of pygidium, with denticulate margin, $\times 4$. 15, Anterior view of cephalon, $\times 4$.



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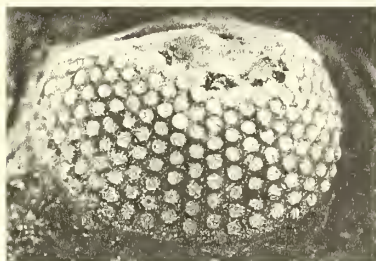
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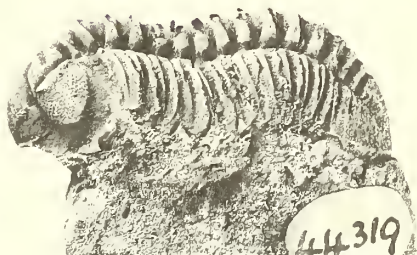
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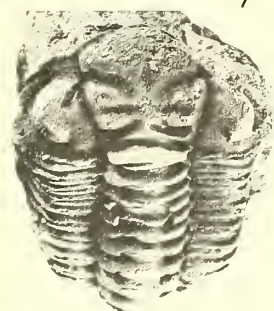
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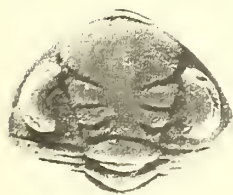
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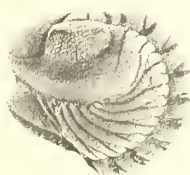
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15

Type Material. Salter (1853, pl. 1, fig. 3) included among his illustrations of *Phacops downingiae* a large-eyed variety from the Wenlock Limestone of Dudley. This specimen, unfortunately, remains untraced but from the figure, the rather bull-nosed frontal lobe and the high occipital ring indicate that it should now be classified as *Acastocephala dudleyensis* sp. nov. rather than *A. macrops* (Salter). In 1864, however, Salter separated the large-eyed *Phacops downingiae* under the variety *macrops* (pl. 2, figs. 26–29). Figs. 26 and 28, from Dudley, again appear to belong to *A. dudleyensis* but these specimens also remain untraced. Of the remaining specimens, fig. 27, from the Wenlock Shale of Malvern, is in the type collection, Birmingham University Museum, No. BU 861, originally from the Ketley Collection. It has been selected here as the lectotype for *A. macrops* on account of its superior preservation to fig. 29 (GSM 19319), an internal mould with damaged pygidium from Pen-y-lan, near Cardiff. Fig. 32 (GSM 19314), was formerly classified by Salter as var. γ , *inflatus* but it seems more probably to be a large specimen of *A. macrops*.

Range and Distribution. Specimens of *A. macrops* collected by Dr. R. B. Grindrod were derived from the Malvern Railway Tunnel. The exact horizon is, therefore, uncertain. However, Symonds and Lambert (1861, p. 158) and Salter (1861, p. 161, appendix to former paper) state that Grindrod's material is from the Woolhope Shales. The possibility of them coming from the Wenlock Limestone or Lower Ludlovian is diminished in the light of further statements by Salter (op. cit.). 'The Wenlock Limestone of this section', he states, 'is not well developed and is cut out in many places by faulting.' When comparing the faunas of the Woolhope Shales and those of the Lower Ludlovian Salter is impressed by the fact that 'In the fewness of Trilobites this shale differs materially from the Woolhope Shale . . .'. It seems most probable, therefore, that all of Grindrod's material is from the Woolhope Shale, Lower Wenlockian.

A. macrops is also recorded from beds of Wenlockian age at Pen-y-lan, Cardiff, and more rarely from the Wenlock Limestone of Dudley. Again the exact horizons at Pen-y-lan are uncertain. Sollas (1879, p. 480) refers the strata of Pen-y-lan quarry to the lowest Wenlockian. The Dudley specimens are generally associated with a blue-grey, calcareous siltstone matrix and are rarely if ever found in the purer limestone bands. They may have been derived either from silty bands within the Wenlock Limestone or from the uppermost Wenlock Shale.

Additional Material. From the Wenlock Shale, Malvern Tunnel; OUM C568, C574, C575, C577, C578, C586, C593, C594, C596, C605, C606, C608; BU 862. From the Wenlock Limestone, Malvern; BM 44411, 58918. From the Wenlock Limestone, Dudley; BM In36155; GSM 19317, 19353; BU (Holcroft) 250. Labelled Wenlock Limestone, Pen-y-lan, Cardiff; BM 44319, 44232. Labelled Wenlock, Pen-y-lan, Cardiff; NMW 14.281.G.14, 40.199.G.7.7. Labelled? Ludlow, Ledbury; NMW 00.312.

Acastocephala dudleyensis sp. nov.

Plate 32, figs. 3–16

Derivation of name. From the type locality of Wren's Nest, Dudley, Wores.

?1853 *Phacops Downingiae* Murchison; Salter, p. 4, pl. 1, fig. 3 (untraced).

?1864 *Phacops (Acaste) Downingiae* Murchison, var. β , *macrops*, Salter, pl. 2, figs. 26 and 28 (specimens untraced).

1965 *Acaste downingiae macrops* (Salter 1864); Clarkson, p. 19, pl. 3, figs. 4–9.

Holotype. BU 863. Wenlock Limestone, Wren's Nest, Dudley, Wores. (ex Holcroft Collection).

Diagnosis. A species of *Acastocephala* with rather strongly convex (sag.) frontal lobe; 3S sigmoidal, similar to *Acaste inflata* (Salter), much more faintly impressed than in *Acastocephala macrops* (Salter); 2S curved both medianly and abaxially to the posterior, longer than in *A. macrops*. Eyes large, situated close to the glabella in adult holaspides, impinging on the posterior border furrows causing them to bulge posteriorly. Visual surface as in *A. macrops* but with one less facet at the maximum height of the surface.

Genae in smallest holaspides with minute postero-lateral projections, rapidly resorbed in succeeding stages. Pygidium as in *A. macrops* but the lateral denticulations are more rapidly resorbed.

Description. Cephalic outline subtriangular, as in *Acaste*. Anterior librigenal projection limited, as in *Acastocephala macrops* (Salter). Surface of test finely granular. Length of cephalon $\frac{1}{2}$ – $\frac{2}{3}$ width.

Glabella anteriorly rounded, more or less laterally subparallel-sided. Degree of tapering in transverse width irregular due to the laterally extensive frontal lobe and the convexity (tr.) of 1L. Frontal lobe both anteriorly and antero-laterally rounded but spreading out laterally; width in relation to 2L and 3L greater than in *A. macrops*; axial furrows deflected abaxially a little at their confluence with 3S instead of running normally round the frontal lobe as a continuation of the line defining 2L and 3L, as is the case in *A. macrops*; rather strongly convex (sag.) in all holaspide stages, bull-nosed, the lateral profile falling steeply to the preglabellar furrow from a point on the sagittal line halfway along the length of the frontal lobe. Outline of frontal lobe in young holaspides more similar to that of the adult *macrops*. 2L and 3L subequal in size, laterally fused in adults but frequently separated in young holaspides. 1L narrow (exsag.), about half the size of 2L, with a greater transverse convexity than that of 2L so that the lateral margins slope below those of 2L, this convexity becoming less in adults. 3S shallow, long sigmoidal, with distinct posterior median deflection, similar to *Acaste* but contrasting with *A. macrops*. 2S shorter, impressed to a similar depth, abaxially linear but with strong median deflection to the posterior; in young holaspides reaching the axial furrows but in adults just failing to do so. 1S wider and deeper than either 2S or 3S, curving both medianly and abaxially to the anterior.

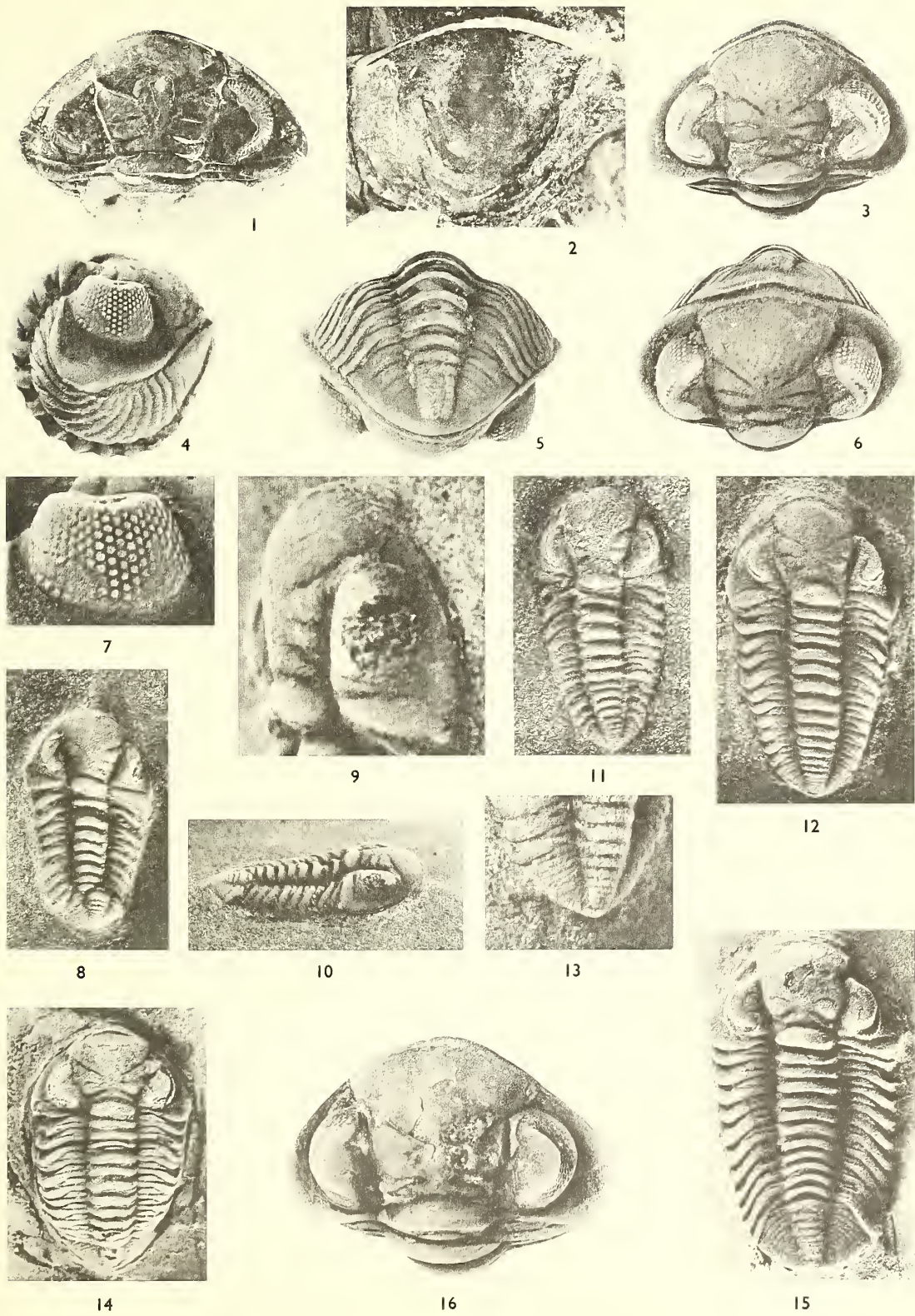
Occipital furrow impressed to similar depth as 1S. Occipital ring narrow (sag.) with similar width and convexity (tr.) to 1L; in lateral profile raised strongly above glabellar side lobes; in young holaspides often with axial node.

Genae, as in *A. macrops*, rather restricted in area due to size and position of eyes. Postocular section of facial suture cutting lateral cephalic margin opposite mid 2L; preocular section dorsal intramarginal, becoming marginal when skirting the antero-lateral margins of the glabella. Genae postero-laterally provided with short projections in small holaspides (with cephalic lengths observed up to about 4.00 mm.); adults with rounded off genal angles.

EXPLANATION OF PLATE 32

Figs. 1–2. *Acastocephala macrops* (Salter 1864). BM 58918; Wenlock Limestone, Malvern, Worcs. 1, Dorsal view of cephalon, $\times 2$. 2, Hypostome, $\times 6$.

Figs. 3–16. *Acastocephala dudleyensis* sp. nov. 3–7. BU 863; Holotype; Wenlock Limestone, Dudley, Worcs. 3, Dorsal view of cephalon, $\times 4$. 4, Lateral view, $\times 4$. 5, Dorsal view of pygidium, $\times 4$. 6, Posterior view of pygidium, $\times 4$. 7, Eye, $\times 8$. 8–10. BU 864; young holaspide. Wenlock Limestone, Dudley, Worcs. 8, Dorsal view, $\times 5$. 9, Genal angle with short projection, $\times 15$. 10, Lateral view, $\times 5$. 11. BU 865; young holaspide. Wenlock Limestone, Dudley, Worcs. Dorsal view, $\times 5$. 12–13. BU 866; young holaspide. Wenlock Limestone, Dudley, Worcs. 12, Dorsal view, $\times 5$. 13, Pygidial margin showing denticulations, $\times 15$. 14. GSM 19311; Wenlock Limestone, Dudley, Worcs. Dorsal view, $\times 3$. 15. BU 867; Wenlock Limestone, Dudley, Worcs. Dorsal view, $\times 3$. 16. BU 868; Wenlock Limestone, Dudley, Worcs. Dorsal view, $\times 3$.



SHERGOLD, *Acastocephala*

Eyes large, crescentic in plan, situated closer to the glabella than to the cephalic margins, on low ocular platform. In lateral profile sloping gently to anterior and rising to the level of the glabella. Extending in adults from occipital furrow or mid 1L to posterior edge of frontal lobe; in young holaspides extending from mid 1L or 1S to confluence of 3S and axial furrows. Palpebral lobe well defined, high; palpebral areas with high inclination to axial furrows. Fixigenal area, between back of eye and posterior border furrow, varying with length of eye; in smallest holaspides H/A is relatively large, 11–27 per cent., but during subsequent growth the eye appears to extend backwards towards the posterior border furrow, H/A decreasing in value, varying in the largest individuals between 3–7 per cent. At this condition the eye abuts against the posterior border furrow and causes it to bulge outwards to the posterior. Table 1 shows the range interval of H/A for arbitrary growth stages, relative age being approximately equated with cephalic length. Variation in A also affects the eye index ratios giving a larger range than would normally be expected; A/G, 52–79 per cent.; A/Gn, 42–62 per cent.

TABLE 1. The range interval for the ratio H/A showing the interval decreasing during the holaspide growth of *Acastocephala dudleyensis* sp. nov., cephalic length being used as a standard.

CLASS RANGE mm.	<i>Acaste downingiae</i>		<i>Acastocephala macrops</i>		<i>A. dudleyensis</i>		<i>Acastoides constricta</i>	
	No	H/A RANGE	No	H/A RANGE	No	H/A RANGE	No	H/A RANGE
1.6–2.6					1	23.20		
2.6–3.6	3	24.14 — 24.81			3	11.11 — 27.44		
3.6–4.6	5	15.38 — 25.10			10	6.40 — 13.66		
4.6–5.6	5	13.33 — 22.56	2	11.11 — 15.28	3	5.55 — 11.76	1	7.31
5.6–6.6	7	15.57 — 20.57	2	8.10 — 12.50	3	4.76 — 8.59	5	7.31 — 12.50
6.6–7.6	10	12.59 — 29.43	1	13.04			11	4.57 — 10.75
7.6–8.6	16	13.57 — 24.92	1	11.72	2	5.31 — 6.39	6	2.96 — 10.00
8.6–9.6	11	12.50 — 24.84	6	7.45 — 16.66	3	3.22 — 6.45	2	4.00 — 8.69
9.6–10.6	12	13.14 — 28.57	7	5.66 — 17.18	1	6.60		
10.6–11.6	10	17.85 — 25.00	4	8.33 — 12.98	1	5.50		
11.6–12.6	9	12.20 — 29.62	4	8.11 — 17.15				
12.6–13.6			1	8.11				

Visual surface overhanging slightly the ocular platform; gently convex outwards; bearing a similar number of lenses to *A. macrops*; at maximum height of the surface, columns of 9 lenses alternate with 8.

Pygidium subtriangular in outline; in posterior profile gently arched. Axis with low or moderate convexity, raised above both axial furrows and pleurae; composed of 7 segments, of which 1–3 are clearly defined, separated by deep transverse furrows and the remainder becoming less distinct posteriorly; postaxial ridge short. Pleurae with rather low convexity (tr.); 4 in number, with frequently a trace of a fifth. Pleural furrows more strongly defined than interpleural furrows but typically weaker than in *Acaste*. Border wide, more extensive in adult holaspides, without appreciable flattening

or furrow. Margin in very small holaspides (observed to a cephalic length of 3.50 mm., and a pygidial length of 1.50 mm.) showing up to 4 pairs of lateral denticulations associated with the posterior bands of pleurae 1-4. These denticulations are rapidly resorbed to give the typically smooth margin of the adult. No traces have been observed of a caudal termination.

Relationships. Adult specimens of *A. dudleyensis* and *A. macrops* may be differentiated by the following characteristics. The frontal lobe of *dudleyensis* is more convex (sag.) than that of *macrops* and appears more laterally extensive; the axial furrows in the former do not diverge evenly; the side furrows of *dudleyensis* are more similar to species of *Acaste* than to *macrops*, the latter has 3S wide and deep and opening out abaxially and 2S short and linear while those of *dudleyensis* are gently curved, reaching, in the adult, nearly to the axial furrows. The eye of *dudleyensis* is closer to the glabella; the posterior border furrow bulges outwards behind the eye; the palpebral areas are less wide and more steeply inclined to the axial furrows; the occipital ring stands higher. Young specimens are more difficult to separate. The occipital ring of *dudleyensis* often bears a median node in the young. A comparison of the rates of resorption of the genal projections and lateral pygidial denticulations shows that these features persist in *A. macrops* to a later ontogenetic stage.

Range and Distribution. *A. dudleyensis* is recorded only from Dudley, Worcs. All the specimens seen by the author are labelled Wenlock Limestone. The matrix associated with all, except enrolled specimens, is, however, always a smooth, bluish or greenish-grey calcareous siltstone, a lithology which may occur as siltstone interleavings within the Wenlock Limestone or in the upper members of the Wenlock Shale. Little can be said, therefore, on the range of this trilobite until the detailed palaeontology and stratigraphy of Dudley is known.

Additional Material. The bulk of the available material is to be found in the Ketley and Holcroft Collections deposited in the Birmingham University Museum. All specimens are from the Wenlock Limestone of Dudley. BU (Holcroft) 48, 50, 102, 295, 440, 474, 541, 548; BU (Ketley) 243, 244, 251; BU (Keeping) 19; also BU 864-8; SM A28693, A 28771; BM In36158-61, 1560; GSM 19311, 19312, 19316.

Acknowledgements. I would like to express my deep gratitude to Dr. J. Shirley for his interest and encouragement at all stages of this work and for his critical reading of the manuscript. I wish also to thank Professor T. S. Westoll for making available the facilities which enabled the work to be completed. I am most grateful to the following for allowing me to borrow specimens in their care and for providing facilities to study their collections; Mr. A. G. Brighton of the Sedgwick Museum, Mr. J. M. Edmonds of the Oxford University Museum, Dr. W. T. Dean and Mr. S. E. Morris of the British Museum (N.H.), Mr. D. E. White of the Geological Survey Museum, Dr. I. Strachan of Birmingham University, Mr. J. Norton of the Ludlow Museum, Dr. M. L. K. Curtis of the Bristol City Museum, and Dr. D. A. Bassett of the National Museum of Wales. I would also like to thank Dr. J. F. Potter of Norwood Technical College for making available specimens from his personal collection.

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OSTRACODA FROM THE UPPER TEALBY CLAY (LOWER BARREMIAN) OF SOUTH LINCOLNSHIRE

by P. KAYE and D. BARKER

ABSTRACT. Thirty-two species and subspecies of Ostracoda are recorded from the Upper Tealby Clay (Lower Barremian) at Dalby Hill, South Lincolnshire. Three species, *Cytherelloidea dalbyensis*, *Amphicytherura bartensteini* and *Orthonotacythere problematica* are considered new; two species are left under open nomenclature. Abundance data are given, and the ranges of the species in other British Lower Cretaceous formations are shown.

SINCE the latter part of last century the Tealby Series of the Wolds of Lincolnshire has been divisible into three on a lithological basis (Judd 1867, 1870; Lamplugh 1896). However, the relationship to the beds above and below is uncertain due to a paucity of fossils and exposures. The three lithologic divisions of the Tealby Series are from the base, the Lower Tealby Clay followed by the Tealby Limestone, and at the top the Upper Tealby Clay. In this account we deal only with the ostracods from the Upper Tealby Clay, the major exposure of which in the South Wolds at the present time is the road cutting at Dalby Hill (G.R. TF/409696). In the course of field mapping during the period 1963-4, J. Newton-Smith of Leicester University brought the roadside section at Dalby Hill to our notice. The ostracods found in the washings of his samples prompted the authors to collect further samples during April 1964. The Upper Tealby Clay is generally a dark clay very rich in limonite oolites; locally it is glauconitic and there are occasional horizons rich in pyrite. Macrofossils obtained from this clay include *Liostrea*, *Oxyteuthis*, and *Aulacotenthis*. The Ostracoda obtained from this horizon are of Lower Barremian age. The specimens described are all deposited in the collections of the British Museum of Natural History (BMNH), London.

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SYSTEMATIC DESCRIPTIONS

Order PODOCOPIDA Müller 1894

Suborder PLATY COPINA Sars 1866

Family CYTHERELLIDAE Sars 1866

Genus CYTHERELLOIDEA Alexander 1929

Cytherelloidea ovata Weber 1934

1934 *Cytherelloidea ovata* Weber, 145, pl. 8, fig. 4.

1950 *Cytherelloidea ovata* Weber; Wolburg, 162.

1963a *Cytherelloidea ovata* Weber; Kaye, 115, pl. 20, figs. 18-21.

Material. A left valve BMNH Io.3048, from the Upper Tealby Clay, Dalby Hill, Lincs.

[Palaeontology, Vol. 9, Part 2, 1966, pp. 208-19, pl. 33.]

Cytherelloidea dalbyensis sp. nov.

Plate 33, figs 1, 2

Holotype. A right valve BMNH Io.3068, from the Upper Tealby Clay, Dalby Hill, Lincs.

Paratype. A right valve BMNH Io.3069, from the same horizon and locality.

Diagnosis. Large *Cytherelloidea*, strongly compressed laterally. Dorsal rib complex, joined both anteriorly and posteriorly to the median rib. Shell surface strongly pitted, almost reticulate.

Measurements. R.V. Holotype Io.3068; length 0.80 mm., height 0.30 mm.

Description. Valves elongate, rather thin and strongly compressed laterally. The dorsal and ventral margins are subparallel but both show a weak concavity centrally in the larger right valves. Anterior margin semicircular, posterior margin rather subquadrate. The lateral surface bears a series of low ribs with shallow depressions between them. Posteriorly the valve is more inflated having a swollen area from which the longitudinal ribs run. Anteriorly there is a crescentic weakly-inflated marginal area equal in width to about one-sixth of the length. This anterior marginal 'strip' merges with the long margins, antero-dorsally and antero-ventrally. Three longitudinal ribs cross the lateral surface, the ventral one being most prominent. This rib runs in a weakly arcuate path a short distance above the ventral margin for the bulk of the length of the valve; posteriorly it is joined to the inflated posterior area but anteriorly it is separated from the marginal strip by a shallow groove. Ventrally from this rib there is a wide marginal shelf. The median rib starts posteriorly at $\frac{3}{4}$ height running horizontally for a short distance and then bifurcates at $\frac{2}{3}$ length. A long ventrally convex portion runs below the muscle pit terminating at $\frac{1}{4}$ length whilst a short upper portion runs dorsally to join the dorsal rib at the mid-length of the valve. The dorsal rib is weak and short; it runs from a position on the dorsal margin at mid-length of the valve obliquely to join the anterior end of the lower branch of the median rib; it is entirely separate from the anterior marginal strip. Between the ribs the valve surface is strongly pitted.

Remarks. *Cytherelloidea dalbyensis* shows strong affinities to *C. elongata* Kaye 1963a from the Middle Barremian of East Yorkshire but is distinct in the pattern of the ribs from any other described Mesozoic species of the genus. From *C. elongata*, *C. dalbyensis* differs in shape and in being much less inflated with the ribs and depressions much less well differentiated; there are also differences in the arrangement of the ribs. In *C. elongata* the ventral rib runs along the margin and is joined anteriorly to a much broader anterior marginal 'strip'. The dorsal rib also runs to join this marginal strip and not the anterior end of the median rib.

Suborder PODOCOPINA Sars 1866
 Superfamily CYTHERACEA Baird 1850
 Family CYTHERIDEIDAE Sars 1925
 Genus DOLOCYTHERIDEA Triebel 1938

Doloccytheridea intermedia Oertli 1958

1958 *Doloccytheridea intermedia* Oertli, 1958, pl. 3, figs. 63–74, pl. 4, figs. 75–82.

1963c *Doloccytheridea intermedia* Oertli; Kaye, 33, pl. 3, figs. 10–14.

Material. A right valve BMNH Io.3051, from the Upper Tealby Clay, Dalby Hill, Lincs.

Genus CLITHROCYTHERIDEA Stephenson 1936

Clithrocytheridea brevis (Cornuel) 1846

1846 *Cythere amygdaloides* var. *brevis* Cornuel, 199, pl. 7, fig. 12.

1956 *Clithrocytheridea brevis* (Cornuel) Deroo, 1510, pl. 11, figs. 15–21.

Material. Five valves BMNH Io.3052, from the Upper Tealby Clay, Dalby Hill, Lincs.

Genus SCHULERIDEA Swartz and Swain

Schuleridea cf. *bernouilensis* Grosdidier 1964

Plate 33, figs. 9, 10

?1964 *Schuleridea bernouilensis* Grosdidier, 225, pl. 1, figs. 2a–g.

Material. Two valves and one carapace BMNH Io.3053–5, from the Upper Tealby Clay, Dalby Hill Lincs.

Remarks. Abundant specimens of a species very closely akin to the French Lower Barremian form *S. bernouilensis* Grosdidier are found at Dalby Hill. Apart from a much poorer development of the eye node in the British material the two forms seem to be identical.

Schuleridea rhomboidalis Neale 1960

1960 *Schuleridea rhomboidalis* Neale, 210, pl. 2, figs. 1, 2, 5, 7, 8.

1963c *Schuleridea rhomboidalis* Neale; Kaye, 32, pl. 3, figs. 1–4.

Material. A right valve BMNH Io.3058, from the Upper Tealby Clay, Dalby Hill, Lincs.

EXPLANATION OF PLATE 33

All figs. $\times 60$; all specimens from the Upper Barremian of Dalby Hill, Lincs.

Figs. 1, 2. *Cytherelloidea dalbyensis* sp. nov. 1, R.V. (Holotype), lateral view; Io.3068. 2, R.V. (Paratype), lateral view; Io.3069.

Figs. 3, 4. *Orthonotacythere problematica* sp. nov. 3, L.V. (Holotype), lateral view; Io.3060. 4, Carapace (Paratype), dorsal view; Io.3061.

Figs. 5–8. *Amphicytherura bartensteini* sp. nov. 5, Female L.V. (Holotype), lateral view; Io.3071. 6, Male R.V. (Paratype), lateral view; Io.3073. 7, Male L.V. (Paratype); lateral view; Io.3072. 8, Female R.V. (Paratype), lateral view; Io.3074.

Figs. 9, 10. *Schuleridea* cf. *bernouilensis* Grosdidier. 9, L.V., lateral view; Io.3053. 10, R.V., lateral view; Io.3054.

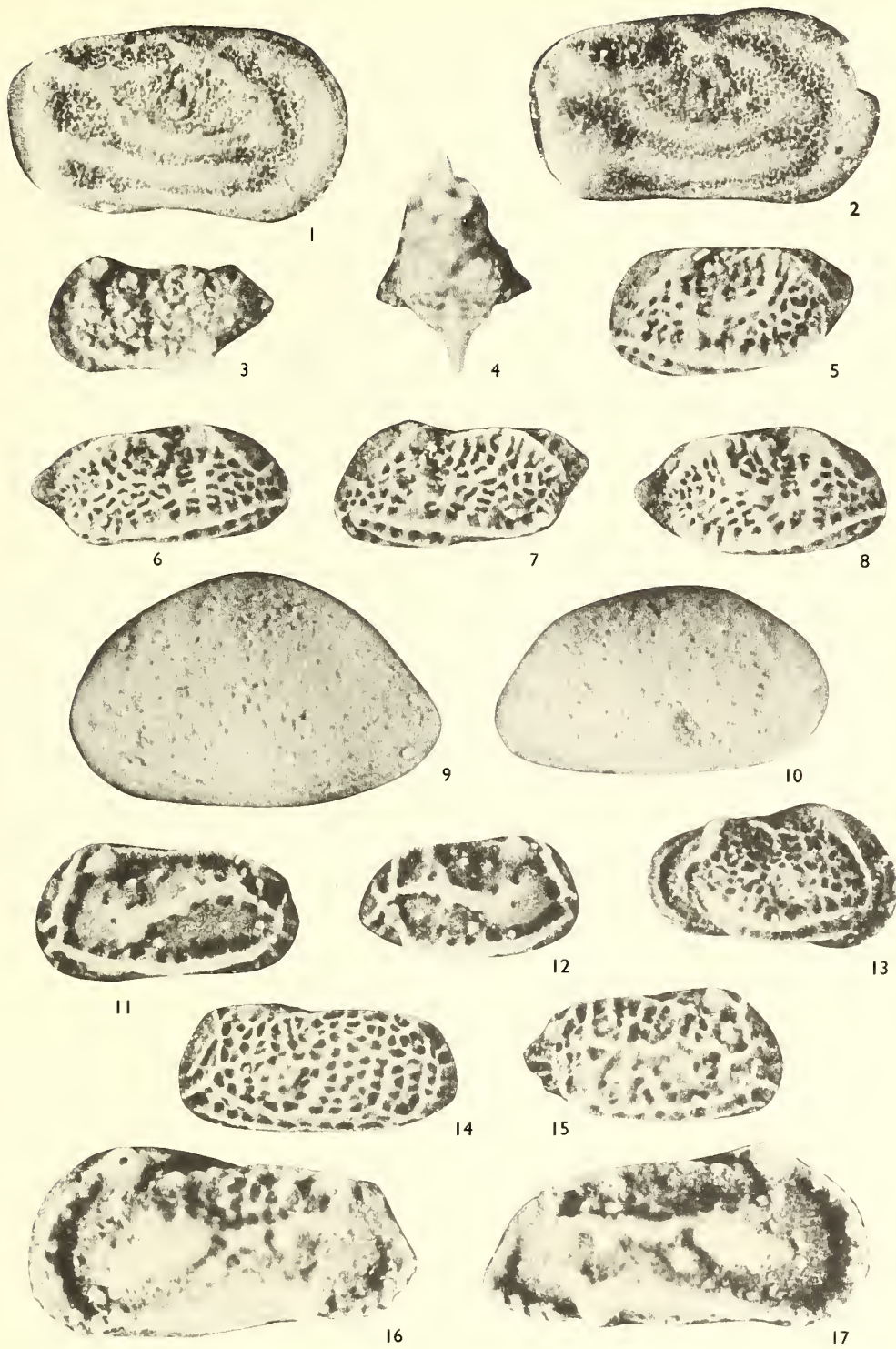
Figs. 11, 12. *Amphicytherura roemeri* (Bartenstein). 11, Male L.V., lateral view; Io.3034. 12, Female R.V., lateral view; Io.3035.

Fig. 13. *Ranocythereis caistorensis* Kaye. R.V. lateral view; Io.3033.

Fig. 14. *Acrocythere haueriviana laeva* Neale. Male L.V., lateral view; Io.3046.

Fig. 15. *Acrocythere haueriviana haueriviana* (Bartenstein). Female R.V., lateral view; Io.3044.

Figs. 16, 17. *Cythereis* cf. *geometrica* Damotte and Grosdidier. 16, Male L.V., lateral view; Io.3063. 17, Male R.V., lateral view; Io.3064.



Genus APATOCY THERE Triebel 1940

Apatocythere ellipsoidea Triebel 19401940 *Apatocythere ellipsoidea* Triebel, 171, pl. 2, figs. 20–26, pl. 9, figs. 104.1956 *Apatocythere ellipsoidea* Triebel; Deroo, 1510.1963c *Apatocythere ellipsoidea* Triebel; Kaye, 32, pl. 3, figs. 5–7.*Material.* A left valve BMNH Io.3056, from the Upper Tealby Clay, Dalby Hill, Lincs.*Apatocythere simulans* Triebel 19401940 *Apatocythere simulans* Triebel, 170, pl. 1, figs. 14–19, pl. 9, fig. 103.1960 *Apatocythere simulans* Triebel; Neale, 210, pl. 2, figs. 1, 2, 5, 7, 8.1963c *Apatocythere simulans* Triebel; Kaye, 32, pl. 3, figs. 1–4.*Material.* A right valve BMNH Io.3057, from the Upper Tealby Clay, Dalby Hill, Lincs.

Genus EURYITYCY THERE Oertli 1959

Euryitycythere sp. B*Material.* A carapace BMNH Io.3070, from the Lower Barremian, Dalby Hill.*Measurements.* Carapace Io.3070; length 0.60 mm., height 0.32 mm.*Remarks.* This extremely rare species is represented by a single closed carapace from Dalby Hill. It is closely related to the Hauterivian species *E. parisiorum* Oertli 1959 but differs in having a crest-like ridge running along the dorsal margin of the larger left valve. This crest also partially overlaps the dorsal margin of the right valve. A further difference is the stronger flattening of the lateral expansion ventrally forming a short blade-like longitudinal rib.

This occurrence is the first record of the genus in the Barremian though a worn but distinctly different specimen has been recorded (Kaye 1965c) from the Upper Aptian of the Isle of Wight.

Family CYTHERURIDAE Müller 1894

Genus AMPHICYTHERURA Butler and Jones 1957

Amphicytherura bartensteini sp. nov.

Plate 33, figs. 5–8

Holotype. A female left valve BMNH Io.3071, from the Upper Tealby Clay, Dalby Hill, Lincs.*Paratypes.* Six valves BMNH Io.3072–5, from the same horizon and locality.*Diagnosis.* *Amphicytherura* with strongly reticulate lateral surface and marked keel-like ventral longitudinal rib.*Measurements.*

	Length	Height
Female L.V. Holotype Io.3071	0.57 mm.	0.30 mm.
Female R.V. Paratype Io.3074	0.57 mm.	0.30 mm.
Male L.V. Paratype Io.3072	0.60 mm.	0.30 mm.

Description. Valves subquadrate in outline, strongly laterally compressed. Dorsal and ventral margins straight and subparallel in the left valves. Anterior margin bluntly rounded, slightly asymmetrical ventrally; posterior drawn out into an acute point at $\frac{2}{3}$ height. Lateral surface bearing a series of ribs. The most prominent is high keel-like, ventrally arcuate, ventral longitudinal; this rib runs from the anterior margin at $\frac{1}{4}$ height across the lateral surface to terminate on the postero-lateral surface at mid-height. A further longitudinal rib runs below this one on the ventral undersurface following a ventrally identical path but reaching the margin postero-ventrally as well as antero-ventrally. A low smooth eye tubercle occurs antero-dorsally bearing a series of weak ribs on its upper surface. These ribs run weakly ventrally and antero-ventrally for a short distance across the lateral surface. A short rib runs from the dorsal margin at mid-length curving towards the posterior margin and terminating at mid-height. A weak node or rudimentary median rib occurs postero-laterally in certain specimens. The whole of the lateral surface is strongly reticulate. Duplicature narrow crossed by few straight radial pore canals. Hinge strongly amphidont, with boss-like divided terminal teeth and strongly divided median furrow in the right valve. Muscle group a row of four oval scars slightly inclined posteriorly with a single small oval scar anteriorly to them opposite the centre of the row.

Remarks. The strong reticulate ornamentation of this species and weak dorsal and median ribbing make it distinct from other members of the genus. It is one of the most abundant ostracods in the Upper Tealby Clay (Lower Barremian) of South Lincs. and is one of the few abundant ostracods from this formation not found in the Lower Tealby Clay and Tealby Limestone (U. Hauterivian) of North Lincs.

Anphicytherura roemeri (Bartenstein) 1956

Plate 33, figs. 11, 12

1956 *Orthonotacythere roemeri* Bartenstein, 531, pl. 3, figs. 76–77.

1965a *Anphicytherura roemeri* (Bartenstein), Kaye, 79, pl. 5, figs. 5–7.

Material. Two valves BMNH Io.3034–5, from the Upper Tealby Clay (Lower Barremian), Dalby Hill, Lincs.

Remarks. This species, characteristic of the Upper Hauterivian in N. Lincs, occurs fairly abundantly in the Lower Barremian of S. Lincs.

Genus EUCYTHERURA Müller 1894

Eucytherura nettletonensis Kaye 1964b

1964b *Eucytherura nettletonensis* Kaye, 321, pl. 55, figs. 5, 6, 8.

Material. Four valves BMNH Io.3040, from the Upper Tealby Clay, Dalby Hill, Lincs.

Genus CYTHERURA Sars 1866

Cytherura reticulosa (Chapman) 1894

1894 *Cytheropteron reticulosum* Chapman, 692, pl. 33, figs. 6a–c.

1964b *Cytherura reticulosa* (Chapman); Kaye, 318, pl. 55, figs. 7, 9.

Material. A left valve BMNH Io.3038, from the Upper Tealby Clay, Dalby Hill, Lincs.

Genus CYTHEROPTERON Sars 1866

Subgenus CYTHEROPTERON Sars 1866

Cytheropteron (Cytheropteron) reightonensis Kaye 1964a1964a *Cytheropteron (C.) reightonensis* Kaye, 102, pl. 5, figs. 1–5.*Material.* A left valve BMNH Io.3039, from the Upper Tealby Clay, Dalby Hill, Lincs.*Cytheropteron (C.) rugosa* Kaye 1965a1965c *Cytheropteron (C.) rugosa* Kaye, 38, pl. 8, figs. 4–5.1965d *Cytheropteron (C.) rugosa* Kaye, Kaye and Barker, 379, pl. 48, fig. 6.*Material.* A left valve BMNH Io.3037, from the Upper Tealby Clay, Dalby Hill, Lincs.

Subgenus EOCYTHEROPTERON Alexander 1933

Cytheropteron (Eocytheropteron) nova Kaye 1964a1964a *Cytheropteron (Eocytheropteron) nova*, Kaye, 104, pl. 5, fig. 6.1965a *Cytheropteron (Eo.) nova* Kaye; Kaye, 75, pl. 5, figs. 18–20.*Material.* Two valves BMNH Io.3062, from the Upper Tealby Clay, Dalby Hill, Lincs.

Subgenus INFRACYTHEROPTERON Kaye 1964a

Cytheropteron (Infracytheropteron) exquisita Kaye 1964a1964a *Cytheropteron (Infracytheropteron) exquisita* Kaye, 105, pl. 5, figs. 9–10.1965 *Cytheropteron (I.) exquisita* Kaye; Kaye and Barker, 380.*Material.* A right valve BMNH Io.3036, from the Upper Tealby Clay, Dalby Hill, Lincs.

Genus ORTHONOTACYTHERE Alexander 1934

Orthonotacythere blanda Kaye 1963e1963e *Orthonotacythere blanda* Kaye, 437, pl. 61, figs. 17, 18.*Material.* A left valve BMNH Io.3043, from the Upper Tealby Clay, Dalby Hill, Lincs.*Orthonotacythere inversa inversa* (Cornuel) 18481848 *Cythere inversa* Cornuel, 244, pl. 1, figs. 12–14.1963e *Orthonotacythere inversa inversa* (Cornuel); Kaye, 435, pl. 61, figs. 1–8, 12, 13.*Material.* A left valve BMNH Io.3042, from the Upper Tealby Clay, Dalby Hill, Lincs.*Orthonotacythere problematica* sp. nov.

Plate 33, figs. 3, 4

1965c *Orthonotacythere* sp. A. Kaye.*Holotype.* A left valve BMNH Io.3060 from the Lower Barremian at Dalby Hill, Lincs.*Paratypes.* One valve and one carapace BMNH Io.3061, from the Lower Barremian at Dalby Hill; 4 valves and 1 carapace BMNH Io. 2070–74, from the basal Atherfield Clay (Lower Aptian) Atherfield, Isle of Wight.

Diagnosis. Small *Orthonotacythere* with tuberculate lateral surface and ventral ridge increasing in height posteriorly. The ventral ridge is drawn out into an alaform spine posteriorly.

Measurements. Holotype, L.V. Io.3060; length 0.47 mm., height 0.25 mm.

Remarks. This species originally described from the Lower Aptian of the Isle of Wight is here named. The Upper Tealby specimens are a little larger than the Aptian ones and have the ventral row of tubercles fused to form a prominent ridge.

Genus ACROCYTHERE Neale 1960

Acrocythere haueriviana haueriviana (Bartenstein) 1956

Plate 33, fig. 15

1956 *Orthonotacythere haueriviana* Bartenstein, 532, pl. 3, fig. 81.

1965a *Acrocythere haueriviana haueriviana* (Bartenstein); Kaye, 78, pl. 5, figs. 12–13.

Material. Two valves BMNH Io.3044–5, from the Lower Barremian, Dalby Hill, Lincs.

Remarks. This characteristic Hauterivian and Lower Barremian subspecies is fairly common at Dalby Hill. The most abundant member of this group in this formation being *A. haueriviana laeva* Neale, the reverse of the situation at Speeton.

Acrocythere haueriviana laeva (Neale) 1960

Plate 33, fig. 14

1960 *Orthonotacythere (Acrocythere) haueriviana laeva* Neale, 213, pl. 3, figs. 10a–b, pl. 4, fig. 13.

1965a *Acrocythere haueriviana laeva* (Neale); Kaye 78, pl. 5, fig. 17.

Material. Two valves BMNH Io.3046–7, from the Upper Tealby Clay (L. Barremian), Dalby Hill, Lincs.

Remarks. This species is extremely abundant at Dalby Hill but is rare at Speeton.

Genus PSEUDOBYTHOCYTHERE Mertens 1956

Pseudobythocythere oruata Kaye 1965a

Material. Three valves BMNH Io.3067, from the Upper Tealby Clay, Dalby Hill, Lincs.

Pseudobythocythere vellicata (Chapman) 1894

1894 *Cytheridea vellicata* Chapman, 690, pl. 33, figs. 3a–c.

1964b *Pseudobythocythere vellicata* (Chapman); Kaye, 323, pl. 54, figs. 14, 17, 18, pl. 55, figs. 10, 11.

1965c *Pseudobythocythere vellicata* (Chapman); Kaye, 42, pl. 8, figs. 14, 15.

Material. Four valves BMNH Io.3066, from the Upper Tealby Clay, Dalby Hill, Lincs.

Family PROGONOCYTHERIDAE Sylvester-Bradley 1948
 Subfamily PROGONOCYTHERINAE Sylvester-Bradley 1948
 Genus NEOCYTHERE Mertens 1956

Neocythere (N.) protovanveeni Kaye 1963b

Material. Four valves BMNH Io.3050 from the Upper Tealby Clay, Dalby Hill.

Subfamily PROTOCYTHERINAE Mandelstam 1960
 Genus PROTOCYTHERE Triebel 1938

Procythere inornata Kaye 1964b

Material. A right valve BMNH Io.3049 from the Upper Tealby Clay, Dalby Hill.

Procythere hechti Triebel 1938

1938 *Procythere hechti* Triebel, 189, pl. 1. figs. 11–16.

1956 *Procythere hechti* Triebel; Deroo, 1513.

1956 *Procythere hechti* Triebel; Bartenstein, 530, pl. 3. figs. 73–75.

1962 *Procythere hechti* Triebel; Neale, 446, pl. 9. figs. 5–7.

Material. A left valve BMNH Io.3059 from the Upper Tealby Clay, Dalby Hill.

Family TRACHYLEBERIDIDAE Sylvester-Bradley 1948
 Genus CYTHEREIS Jones 1849

Cythereis blanda Kaye 1963d

Material. Two valves BMNH Io.3041 from the Upper Tealby Clay, Dalby Hill.

Cythereis cf. *geometrica* Damotte and Grosdidier 1963

Plate 33, figs. 16, 17

Material. Five valves and one carapace BMNH Io.3063–5 from the Upper Tealby Clay, Dalby Hill.

Remarks. Specimens related to *C. geometrica* Damotte and Grosdidier 1963 occur abundantly in the Upper Tealby Clay. The major difference between the two species is the stronger development of the median longitudinal ridge in the Lower Barremian forms. This feature shows similarities to *C. geometrica fittoni* Kaye 1965c from the Upper Aptian of the Isle of Wight but the Lincolnshire specimens lack the strong surface reticulation of the latter species. It is possible that the Lower Barremian forms are ancestral to the Aptian species.

Genus RANOCYTHEREIS Kaye 1965b
Ranocythereis caistorensis Kaye 1965b

Plate 33, fig. 13

Material. A right valve BMNH Io.3033 from the Upper Tealby Clay, Dalby Hill, Lincs.

Remarks. This species, previously recorded from the Lower Tealby Clay and Tealby Limestone (Hauterivian) of Nettleton, N. Lincs., occurs moderately rarely at Dalby Hill.

CONCLUSIONS

The Upper Tealby Clay at Dalby Hill is rich in ostracoda, both in numbers of individuals, and in number of species. The relative abundances of the thirty-two species and subspecies recorded are summarized as follows:

Abundant

Clithrocytheridea brevis (Cornuel); *Eucytherura nettletonensis* Kaye; *Schuleridea* cf. *bernouilensis* Grosdidier; *Amphicytherura bartensteini* sp. nov.; *Acrocythere haueriviana laeva* Neale; *Pseudobythocythere ornata* Kaye; *Pseudobythocythere vellicata* (Chapman); *Neocythere* (N.) *protovanveeni* Kaye; *Protocythere hechti* Triebel; *Cythereis blanda* Kaye; *Cythereis* cf. *geometrica* Damotte and Grosdidier.

Common

Schuleridea rhomboidalis Neale; *Apatocythere ellipsoidea* Triebel; *Amphicytherura roemeri* (Bartenstein); *Cytheropteron* (Eo.) *nova* Kaye; *Acrocythere haueriviana haueriviana* (Bartenstein).

Frequent

Cytherelloidea ovata Weber; *Apatocythere simulans* Triebel; *Dolocytheridea intermedia* Oertli; *Orthonotacythere inversa inversa* (Cornuel); *Protocythere triplicata* (Roemer); *Ranocythereis caistorensis* Kaye.

Rare

Cytherelloidea dalbyensis sp. nov.; *Bairdia* sp.; *Cytherura reticulosa* (Chapman); *Cytheropteron* (C.) *reightonensis* Kaye; *Euryitycythere* sp. B.; *Cytheropteron* (C.) *rugosa* Kaye; *Cytheropteron* (Infra.) *exquisita* Kaye; *Orthonotacythere blanda* Kaye; *Orthonotacythere problematica*; *Protocythere inornata* Kaye.

The known range of the Upper Tealby Ostracoda and their geographical occurrence in England are shown in text-fig. 1.

The Upper Tealby fauna is Lower Barremian in age; with such species as *Orthonotacythere blanda*, *O. inversa inversa* and, *Pseudobythocythere ornata* being only known previously from beds at this horizon at Speeton, E. Yorks. The fauna as a whole shows strong affinities to the lithologically similar Upper Hauterivian at Nettleton in N. Lincs., seventeen of the species recorded at Dalby Hill being also known from Nettleton; Lower Barremian strata are absent in N. Lincs. The clays of Upper Hauterivian and Lower Barremian age at Speeton differ markedly from those at Dalby, lacking the glauconite and iron carbonate oolites. Nine species found at Dalby Hill occur in higher Barremian horizons at Speeton; the known range of one (*Cythereis blanda*) being extended down into the Lower Barremian. Four Hauterivian species: *Eucytherura nettletonensis*, *Amphicytherura roemeri*, *Acrocythere haueriviana laeva*, and *Ranocythereis caistorensis* have their known ranges extended up into the Lower Barremian whilst

SPECIES	UPPER HAUTERIVIAN		BARREMIAN			APTIAN	
	UPPER		LOWER		M & U	L & U	UPPER
	Nettleton N. Lincs.	Speeton E. Yorks.	Dalby Hill S. Lincs.	Speeton E. Yorks.	Speeton E. Yorks.	South East England	Suttersby S. Lincs.
<i>Cytherellaidea dalbyensis</i> nov.			X				
<i>Cytherellaidea avata</i> Weber.	X	X	X	X	X	X	X
<i>Bairdia</i> sp.			X				
<i>Clithracytheridea brevis</i> (Carnuel).			X				
<i>Dalacytheridea intermedia</i> Oertli.	X	X	X	X	X		
<i>Schuleridea</i> cf. <i>bernauilensis</i> Grasdier.			X				
<i>Schuleridea rhomboidalis</i> Neale.	X	X	X	X			
<i>Apatacythere ellipsaidea</i> Triebel.	X	X	X	X	X		
<i>Apatacythere simulans</i> Triebel.	X	X	X	X			
<i>Euryiticythere</i> sp. B.			X				
<i>Cytherura reticulosa</i> (Chapman).	X		X			X	X
<i>Eucytherura nettletanensis</i> Kaye.	X		X				
<i>Amphicytherura bartensteini</i> nov.			X				
<i>Amphicytherura raemeri</i> (Bartenstein).	X		X				
<i>Cytherapteran</i> (C) <i>reighanensis</i> Kaye.			X	X	X		
<i>Cytherapteran</i> (C) <i>rugosa</i> Kaye.	X		X			X	X
<i>Cytherapteran</i> (Ea) <i>nava</i> Kaye.	X	X	X	X	X		
<i>Cytherapteran</i> (Infra) <i>exquisita</i> Kaye.			X	X	X	X	X
<i>Orthanatacythere inversa inversa</i> (Carnuel).			X	X			
<i>Orthanatacythere blanda</i> Kaye.			X	X			
<i>Orthanatacythere problematica</i> nov.			X				
<i>Pseudabythacythere ornata</i> Kaye.	X		X	X			
<i>Pseudabythacythere vellicata</i> (Chapman).			X			X	
<i>Acracythere hauteriviana hauteriviana</i> (Bartenstein).	X	X	X	X			X
<i>Acracythere hauteriviana laeva</i> Neale.	X	X	X				
<i>Neacythere</i> (N) <i>pratavanveeni</i> Kaye.	X		X	X	X		
<i>Protocythere inornata</i> Kaye.			X			X	
<i>Pratacythere hechti</i> Triebel.	X	X	X	X			
<i>Pratacythere triplicata</i> (Raemer).	X	X	X	X	X		
<i>Cythereis blanda</i> Kaye.			X		X	X	
<i>Cythereis</i> cf. <i>geometica</i> D&G.			X			X	
<i>Ranacythereis caistarensis</i> Kaye.	X		X				

TEXT-FIG. 1. Known distribution of Ostracoda found in the Upper Tealby Clay at Dalby Hill.

the ranges of *Pseudobithocythere vellicata* and *Protocythere inornata* are extended down into the Lower Barremian. Two already described species, *Clithrocytheridea brevis* and *Schuleridea bernoullensis* are recorded from England for the first time.

There is surprisingly little relationship between the fauna of the Upper Tealby Clay and the Upper Aptian Sutterby Marl formation. Only five species are common to the two, none of which are abundant at Sutterby. Stronger ties are found with the Aptian of South-east England, eight species occurring there and at Dalby Hill. None of the species extend into post-Aptian sediments.

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THE FORAMINIFERAL GENUS *BOLIVINOIDES* FROM THE UPPER CRETACEOUS OF THE BRITISH ISLES

by F. T. BARR

ABSTRACT. Nine species of *Bolivinoides* are described from the Upper Cretaceous (Santonian to Lower Maestrichtian) strata of the British Isles, and their stratigraphical ranges are recorded in relation to the classical megafossil zonation. Three of these species, *Bolivinoides hiltermanni*, *B. praelaevigata*, and *B. sidestrandensis*, are described as new and a lectotype is proposed for *B. decorata* (Jones). The phylogeny of various lineages of the genus *Bolivinoides* is discussed.

DURING the last fifteen years, a series of important studies has been published on the Upper Cretaceous–Lower Tertiary foraminiferal genus *Bolivinoides* Cushman. In Germany, Hiltermann (1952, 1963) and Hiltermann and Koch (1950, 1955, 1960, 1962) have published a number of valuable works demonstrating the stratigraphical value of *Bolivinoides* in strata of Santonian to Danian age. The usefulness of this group has been shown by Edgell (1954) in Australia, Reiss (1954) in the Middle East, Pożaryska (1954) in Poland, and Vassilenko (1961) in the Soviet Union. The stratigraphical ranges of many species of this rapidly evolving group appear to be almost identical over much of the world. Consequently, some lineages of *Bolivinoides* have proved to be extremely useful in intercontinental correlations within the upper part of the Upper Cretaceous.

The Upper Cretaceous Chalk of the British Isles usually contains abundant and diverse foraminiferal faunas. In strata of Santonian to Maestrichtian age, various species of *Bolivinoides* are often an important element of this fauna. A number of short publications mentioned the presence of one or more of these species in the British Upper Cretaceous, but no attempt had been made to monograph this group or to establish their usefulness in the precise dating of the Upper Cretaceous Chalk in the British Isles. Wright (1886) originally described *Bolivinoides decorata* from the Upper Campanian of Keady Hill, Northern Ireland. In a short note, Chapman (1892) described *B. strigillata* for the first time from the Santonian phosphatic chalk at Taplow in Buckinghamshire. *B. decorata* was recorded by Heron-Allen and Earland (1910) from the interior of a flint nodule found on the beach at Selsey Bill, Sussex. Williams-Mitchell (1948, p. 106, pl. 9, fig. 3, pl. 10) illustrated a specimen of *B. decorata* from southern England which he misidentified as *B. strigillata* (Chapman). In an important work on the Upper Cretaceous Foraminifera from Northern Ireland, McGugan (1957) recorded and illustrated specimens identified as *B. decorata* and *B. draco* (Marsson) from the Ballycastle Pellet Chalk. Curry (1962) recorded several species of *Bolivinoides* from submarine cores taken from the English Channel, but none of the specimens were illustrated or described. Recently, Barr and Cordey (1964) re-examined Chapman's (1892) material and proposed a lectotype for *B. strigillata*.

The purpose of the present paper is to describe the various species of *Bolivinoides* found in the British Isles and to record their stratigraphical ranges, which can be

compared with the classical Upper Cretaceous megafossil zonation recognized in western Europe. It is hoped that this study will aid in the precise dating and correlation of the Upper Cretaceous strata of the British Isles and further our understanding of the evolution of certain lineages of the genus *Bolivinoides*.

Deposition of types. The lectotype and syntypes of *Bolivinoides decorata* (Jones) are housed in the Joseph Wright Collection in the Department of Zoology, Queen's University, Belfast, Northern Ireland. Illustrated topotype specimens of *Bolivinoides decorata australis* Edgell are located in the Commonwealth Paleontological Collection, Bureau of Mineral Resources, Canberra, Australia. All other holotypes, paratypes and hypotypes illustrated in this paper are deposited in the British Museum (Natural History), London. Additional paratypes of *B. hiltermanni*, *B. praelaevigata*, and *B. sidestrandensis* will be deposited in the foraminiferal collections of the U.S. National Museum, Washington, D.C.

Acknowledgements. I would like to thank Dr. Tom Barnard for his help in many aspects of this study; Drs. H. Hiltermann and Z. Reiss for their helpful suggestions; Miss Anne Cameron, for the loan of material from the Joseph Wright Collection; Dr. N. H. Fisher, for sending type material from Edgell's Collection; Dr. R. E. H. Reid, who furnished material from the Ballycastle Pellet Chalk and gave helpful information concerning Irish stratigraphy and the location of old foraminiferal collections in Northern Ireland; Dr. A. McGugan, who sent material from Northern Ireland; Mr. S. V. Bell for help in collecting the Norwich and Sidestrand localities; Dr. W. A. Berggren, who drew my attention to several important Russian studies; and also my wife Melza, for preparing the illustrations of foraminifera used in this paper.

STRATIGRAPHY

The Upper Cretaceous Chalk forms many prominent outcrops in southern England and the excellently exposed sea cliff sections often represent continuous deposition from Cenomanian to Upper Campanian times. Chalk of Maestrichtian age is present only in a few small outcrops along the Norfolk coast (i.e. Trimmingham, Sidestrand). Over much of southern England, Upper Campanian strata have been truncated by a Lower Tertiary unconformity. Samples used in the present study were collected from various localities in southern England, Northern Ireland and Eire. Stratigraphic sections were measured and collected at Culver Cliff, on the east coast of the Isle of Wight (see text-figs. 2, 3), and at Alum Bay, on the opposite side of the island. The stratigraphy of the Culver Cliff section has already been described (Barr 1962). Most of the sample localities had been previously dated by megafossils and placed in the classical zonation that has been used in England and parts of western continental Europe for over half a century (see text-fig. 1).

One of the earliest successful attempts to zone the Upper Cretaceous rocks of the British Isles was made by Barrois (1876). He completed a comprehensive study of the Upper Cretaceous rocks of England and Ireland and showed that it was possible to recognize the same megafossil zones in the British Isles as were established in the Upper Cretaceous of France, and that these zones could be grouped into the Cenomanian, Turonian and Senonian Stages proposed by d'Orbigny (1842, 1852). This zonation has since been modified and refined by Jukes-Browne (1904, 1912), Rowe (1908), Brydone (1914), Jeletzsky (1951), and others, but still forms the basis for the present megafossil zonation of the British Upper Cretaceous.

Maestrichtian Stage. The Maestrichtian Stage was originally proposed by Dumont (1849). Its type section is located in the E.N.C.I. Quarry at St. Petersburg on the

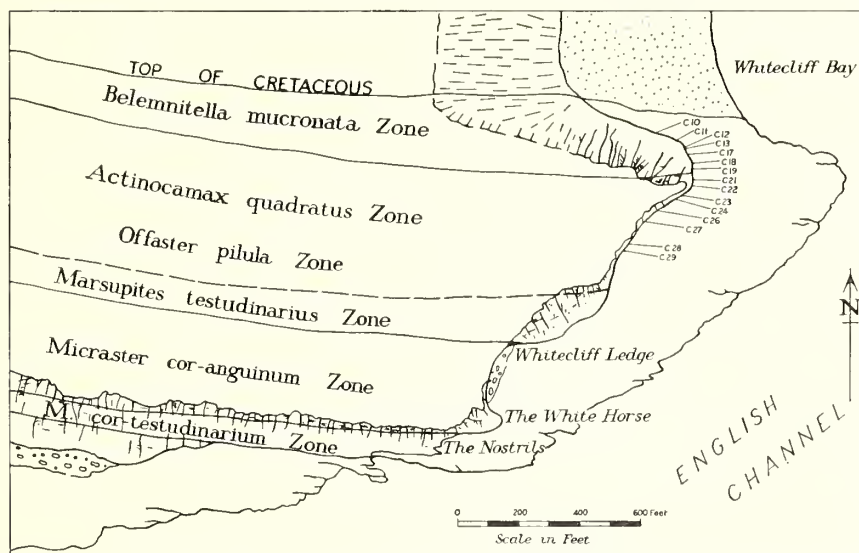
outskirts of Maastricht, Netherlands. In recent years the literature on the type section and correlation of the Maestrichtian Stage has been voluminous and sometimes contradictory. However, it is now generally accepted that the Maestrichtian Stage should be

STAGE		Z O N E		GROUP	FORMATION
S E N O N I A N	M A E S T R I C H T I A N	Upper	Belemnitella casimirovensis	U P P E R C H A L K	Not present in England
			Belemnitella junior		
		Lower	Ostrea lunata		
	Belemnitella lanceolata (s.s.)				
	C A M P A N I A N	Upper	Belemnitella mucronata		
		Lower	Actinocamax quadratus		
	S A N T O N I A N	? ?	Offaster pilula		
			Marsupites testudinarius		
			Microaster cor-anguinum		
			Microaster cor-testudinarium		
T U R O N I A N		Holaster planus	M I D D L E C H A L K	Chalk Rock	
		Terebratulina lata		"Chalk without Flints"	
		Inoceramus labiatus (Rhynchonella cuvieri)		Melbourn Rock	
C E N O M A N I A N	Upper	Holaster subgloboso	L O W E R C H A L K	Plenus Marl	
		Schloenbachia varians		Grey Chalk	
	Lower				Totternhoe Stone
				Chalk Marl	
				Glauconitic Marl	

TEXT-FIG. 1. Chart showing megafossil zonation of the Upper Cretaceous strata of the British Isles.

regarded as the uppermost Cretaceous stage, underlying the Danian Stage of Desor (1846), which is now regarded as lowermost Tertiary, and overlying either the Senonian Stage of d'Orbigny (1842, 1852) or the Campanian Stage of Coquand (1857). The Maestrichtian Stage can be subdivided on the basis of belemnites into four or more zones which can be recognized in its type area and over much of western Europe.

The only chalk of Maestrichtian age found in England is in a few small outcrops exposed along the Norfolk coast, including some large erratic blocks. Jukes-Browne (1904) and Brydone (1906, 1908) published a series of papers on these exposures in which they recognized a different fauna from that found in the Norwich Chalk or the youngest chalk found along the south coast of England. They concluded that these outcrops represented the youngest known Upper Cretaceous strata found in England. Jukes-Browne (1904) proposed the Zone of *Ostrea lunata* to include the chalk at Trimingham. Jeletzky (1951) made a study of the belemnites from the Trimingham and



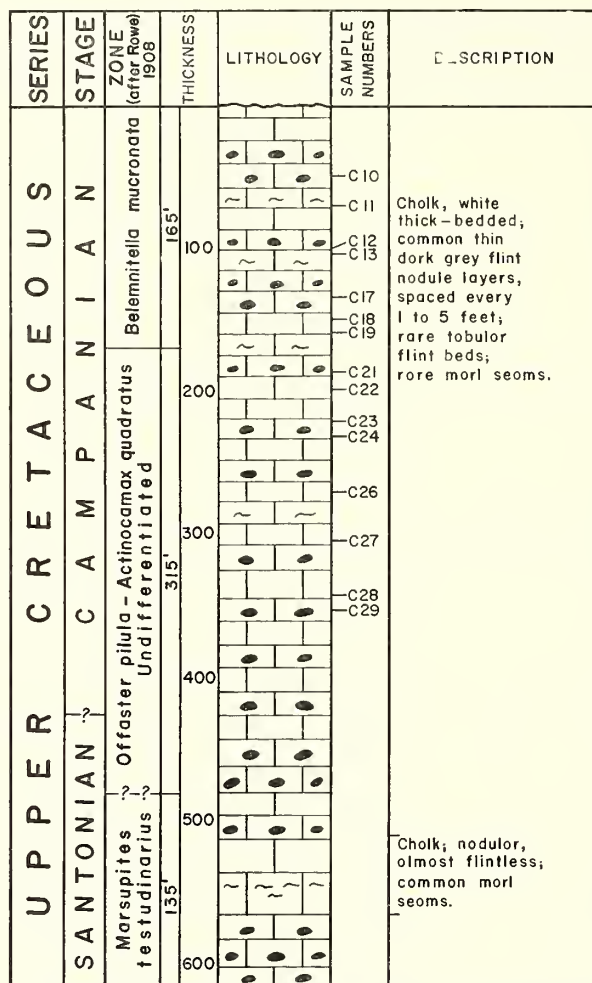
TEXT-FIG. 2. Location map of Culver Cliff on the east-central coast of the Isle of Wight showing position of samples. Zones after Rowe (1908).

Norwich Chalk and concluded that the Trimingham Chalk was Lower Maestrichtian in age and should be assigned to the *Belemnitella lanceolata* (s.s.) and *Belemnitella lanceolata sumensis* Zones (which are also recognized in the type area of the Maestrichtian Stage), whereas the Norwich Chalk contained *Belemnitella mucronata* and was Upper Campanian. Jukes-Browne's Zone of *Ostrea lunata* was found to be equivalent to the combined zones of *B. lanceolata* (s.s.) and *B. lanceolata sumensis*.

Campanian Stage. Coquand (1857, 1858), in a study of the Cretaceous stratigraphy of the northern Aquitaine Basin, proposed the erection of three stages, the Campanian, Santonian and Coniacian, which are equivalent to the Senonian Stage of d'Orbigny. The type locality of the Campanian Stage is in south-west France near Aubeterre, while the type locality of the Senonian Stage is in the Paris Basin (d'Orbigny 1842, 1852). Through the years the Campanian, Santonian, and Coniacian have been regarded as substages of the Senonian; however, over the last one or two decades, there has been a tendency to use Coquand's units as stages and to drop the broader term Senonian. Unfortunately, the type sections of these stages are not well known and the exact position of the boundaries between these stages is not always certain. This is partially

responsible for Coquand's stages not being accepted in the Gulf Coast area of the U.S.A., where the local stage names Navarro, Taylor, and Austin are in use.

The Campanian Stage is subdivided into two belemnite zones, the *Belemnitella mucronata* Zone and the *Actinocamax quadratus* Zone, which are regarded as equivalent to the



TEXT-FIG. 3. Columnar section of upper part of the Upper Chalk at Culver Cliff, Isle of Wight, showing stratigraphic position of samples.

Upper and Lower Campanian respectively. Jeletzsky (1951) presented cogent reasons for placing the Maestrichtian-Campanian boundary at the top of the *B. mucronata* Zone rather than within this zone as has sometimes been done (Barnard and Banner 1953, p. 207; Curry 1962, p. 181).

Santonian Stage. The Santonian Stage was erected by Coquand (1857, 1858), with the type locality near the town of Saintes in the northern Aquitaine Basin. The limits of this

stage have not been well defined, and consequently there is considerable disagreement as to what constitutes the Lower Santonian in north-western Europe and the British Isles. In Britain, the Santonian–Coniacian contact is usually placed at the base of the *Marsupites testudinarius* Zone (Barnard and Banner 1953; Barnard 1963; Barr 1962; Curry 1962). On the other hand, many continental stratigraphers (e.g. Gignoux 1955, p. 392) include the *Micraster cor-anguinum* Zone in the Lower Santonian and place the Santonian–Coniacian contact at the base of the *M. cor-anguinum* Zone. This difference can only be resolved when the type sections of the Santonian and Coniacian Stages become better known and when exact correlations are possible between the Anglo-Paris Basins and the northern Aquitaine Basin. One must keep this difference in mind when comparing the stratigraphical ranges of fossils recorded from various parts of Europe.

PHYLOGENY

A number of papers have dealt with the phylogeny of certain species or lineages of *Bolivinoides*. The works of Hiltermann and Koch (1950), Edgell (1954), Reiss (1954), Hofker (1957, 1958a, 1958b), Vassilenko (1961), and Hiltermann (1963) have shown evolutionary development in this group to be similar in various parts of the world. Consequently, the recognition of these evolutionary sequences within the genus *Bolivinoides* can be extremely useful in the correlation and dating of Upper Cretaceous

STAGE	C A M P A N I A N														
	U P P E R							L O W E R							
ZONE	B. mucronata							A. quadrotus							
SAMPLE	C10	C11	C12	C13	C17	C18	C19	C21	C22	C23	C24	C26	C27	C28	C29
SPECIES															
B. laevigata	■			○											
B. decorata		○													
B. praelaevigata		○	●				●								
B. pustulata								○	○	○	○				
B. hiltermanni								○					○	○	○

COMMON

●

FEW

○

RARE

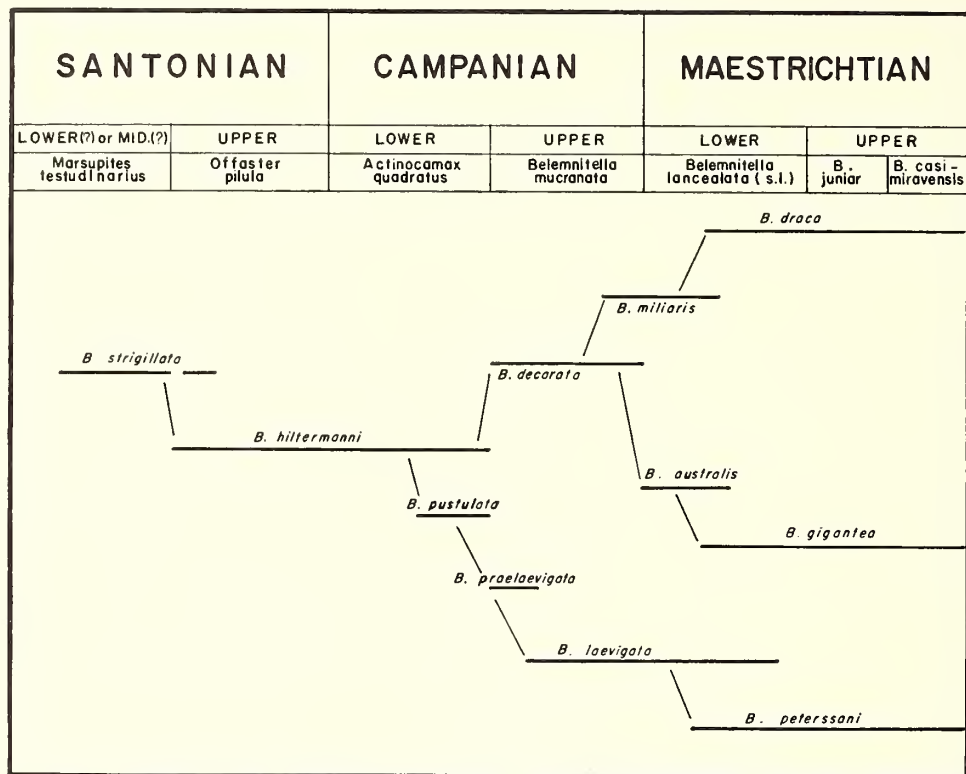
■ COMMON ● FEW ○ RARE

TEXT-FIG. 4. Chart showing distribution of *Bolivinoides* in the Campanian chalk at Culver Cliff, Isle of Wight.

strata. However, there is not complete agreement as to the phylogeny of all *Bolivinoides* lineages and it has been suggested (Hiltermann 1963) that subspecific differences may exist within some evolutionary lineages in different geographic provinces. The Upper Cretaceous Chalk of the British Isles provides an excellent opportunity to observe the development of some lineages of *Bolivinoides* and it is hoped that these observations will help clarify some of the phylogenetic relationships of this group.

Bolivinoides strigillata (Chapman) appears to be restricted to the *Marsupites testudinarius* Zone (Lower or Middle Santonian) and possibly the basal part of the *Offaster pilula* Zone. It is the oldest species of *Bolivinoides* recognized in the British Isles or elsewhere in the world, and from this species evolved the various lineages that are so common higher in the Upper Cretaceous strata. *B. strigillata* (s.s.) is usually quite rare, but the many forms which rapidly evolved from this ancestral species became increasingly abundant and diversified later in the Upper Cretaceous. The genus *Bolivinoides*

reached its acme in the Maestrichtian and survived into the Danian, but with progressively fewer individuals.



TEXT-FIG. 5. Diagram showing the stratigraphic ranges and suggested phylogeny of various species of *Bolivinoides*.

The most common lineage of *Bolivinoides* observed in the British Isles commences with *B. strigillata* and evolves through *B. hiltermanni* sp. nov., *B. decorata* (Jones) to *B. miliaris* Hiltermann and Koch. The end member of this lineage, *B. draco* (Marsson), was not found, as the Upper Maestrichtian is not present in Britain, nor was the *B. australis*–*B. gigantea* offshoot observed. The *B. strigillata*–*B. gigantea* lineage shows several progressive changes in morphology: an increase in overall size; smaller length/breadth ratios; and an increase in the number of ‘ornamental’ lobes on the final chambers. The evolution of *B. decorata* to *B. miliaris* to *B. draco* produces a progressively more rhomboidal or kite-shaped test and the development of medial ribs. *B. decorata* has often been regarded as evolving directly from *B. strigillata* (Hiltermann and Koch 1950; Vassilenko 1961; Hiltermann 1963). However, in the well-developed Lower Campanian section in southern England a transitional species, *B. hiltermanni* sp. nov., is found in considerable abundance. This species is intermediate in size and in strength of ornamentation between *B. strigillata* and *B. decorata*.

There is also an indication that *B. hiltermanni* is probably the ancestral species to the *B. pustulata* Reiss–*B. praelaevigata* sp. nov.–*B. laevigata* Marie–*B. peterssoni* Brotzen

lineage. *B. hiltermanni* has a thicker, less compressed test than species of the *B. pustulata*–*B. peterssoni* lineage; however, variants of this species found in the upper part of the *Actinocamax quadratus* Zone may represent an intermediate form between *B. hiltermanni* (s.s.) and *B. pustulata*, although the complete transition of forms was not observed. The *B. pustulata*–*praelaevigata*–*laevigata*–*peterssoni* lineage is characterized by a small compressed test with rather weakly developed ornamentation chiefly restricted to the medial part of the test.

SYSTEMATIC PALAEOLOGY

Order FORAMINIFERIDA

Superfamily BULIMINACEA Jones 1875

Family BOLIVINITIDAE Cushman 1927

Genus BOLIVINOIDES Cushman 1927

Type Species. Bolivinoides draco (Marsson).

Description. Test completely biserial, gradually tapering to flaring, with greatest breadth usually near apertural end, and circular or elliptical in cross section. Proloculus globular, smooth. Chambers inflated, curved, uniformly and fairly rapidly increasing in size with greatest height and thickness near longitudinal axis. Sutures often obscure, slightly curved. Aperture a slit-like or loop-shaped opening near centre of apertural face, often bordered by weakly developed lip and with internal tooth plate structure. Ornamentation usually strongly developed, consisting of lobes and knobs running perpendicular to sutures. Internal wall surface also contains semi-conical bulges. Wall calcareous, finely perforate.

Remarks. Numerous specimens of *Bolivinoides* were serially sectioned and their internal structure examined. The present study confirms many of Montanaro Gallitelli's (1957, pp. 145, 146) observations. She examined the internal structure of acid treated specimens of *Bolivinoides draco* (Marsson) and observed that the internal surface of the test had a tuberculate sculpture. The internal surface of the tests of all species sectioned in the present study contained semi-conical bulges along the base of the chambers. In species such as *B. draco* with strongly developed, but fine external ornamentation, the internal circular bulges occupy most of the chamber walls in the earliest chambers and occupy somewhat less in the final chambers. In most of the other species, however, the internal bulges are restricted to about the lower quarter of the chamber surface. The maximum breadth of the bulge is along the lower suture. These internal knobs correspond to the depressed areas between lobes on the external surface. In fact, almost all of the external 'ornamental' lobes and knobs are reflected interiorly, producing a partially corrugated test wall (see text-figs. 7, 8). These observations do not agree exactly with those of Reyment (1959, p. 13) who stated that the tuberculated wall structure seen by Montanaro Gallitelli was derived from cameral overlaps. The external sculpture, and concomitantly the internal sculpture, of *Bolivinoides* therefore appears to represent structure more fundamental than the more usual surface ornamentation of many genera, which is sometimes quite superficial.

An internal bolivine tooth plate structure was observed in *Bolivinoides*, similar to that described by Hofker (1957) and Reyment (1959).

Bolivinoides strigillata (Chapman)

Plate 34, figs. 8, 9; Plate 37, figs. 7-9

Bolivina strigillata Chapman 1892, p. 515, pl. 15, fig. 10.*Bolivinoides strigillata* (Chapman); Hiltermann and Koch 1950, pp. 614-23, text-figs. 2 (1-19), 3 (1-9), 5 (10).*Bolivinoides strigillata* (Chapman); Edgell 1954, pp. 70, 71, pl. 13, fig. 8; pl. 14, fig. 9.*Bolivinoides strigillatus* (Chapman); Bykova 1959, table 1, fig. 1.*Bolivinoides strigillata* (Chapman); Vassilenko 1961, pp. 186-8, pl. 39, figs. 7a-c.*Bolivinoides strigillata* (Chapman); Hiltermann 1963, pp. 209, 210, pl. 1, figs. 12-14, 16, 18, 19, 24.*Bolivinoides strigillata* (Chapman); Barr and Cordey 1964, pp. 308, 309, pl. 49, figs. 1-3.

Description. Test biserial, elongate, sides gradually tapering, subelliptical to oval in cross section; proloculus globular, followed by 6 to 8 pairs of indistinct, slightly inflated chambers uniformly and gradually increasing in size; sutures slightly oblique, indistinct, obscured by ornamentation; 2 or 3 weakly raised lobes on final chambers running perpendicular to sutures, ornamentation on earliest chambers less distinct, sometimes surface of early part of test smooth; aperture a slit-like opening between lobes on final chamber; wall calcareous, finely perforate; length/breadth ratio 1.7 to 2.2; breadth/thickness ratio 1.4 to 1.9; approximate average length of adult specimen 0.40 mm.

Remarks. *Bolivinoides strigillata* is the most primitive species known of the genus *Bolivinoides*, and the only species found in strata as old as the *Marsupites testudinarius* Zone in the British Isles. It is one of the smallest species of *Bolivinoides* and appears to be the ancestral species of several of the most common and stratigraphically important lineages of this genus (see text-fig. 5).

Chapman (1892, p. 515) originally described *B. strigillata* from the phosphatic chalk at Taplow, Buckinghamshire. Barr and Cordey (1964, p. 308) collected additional material from Taplow and re-examined Chapman's original specimens, which are deposited in the British Museum (Natural History). They redescribed *B. strigillata* and proposed a lectotype for this species from syntypic specimens in the Chapman Collection (BM P44968).

A single specimen referred to *Bolivina strigillata* Chapman by Williams-Mitchell

EXPLANATION OF PLATE 34

All illustrations unretouched photographs.

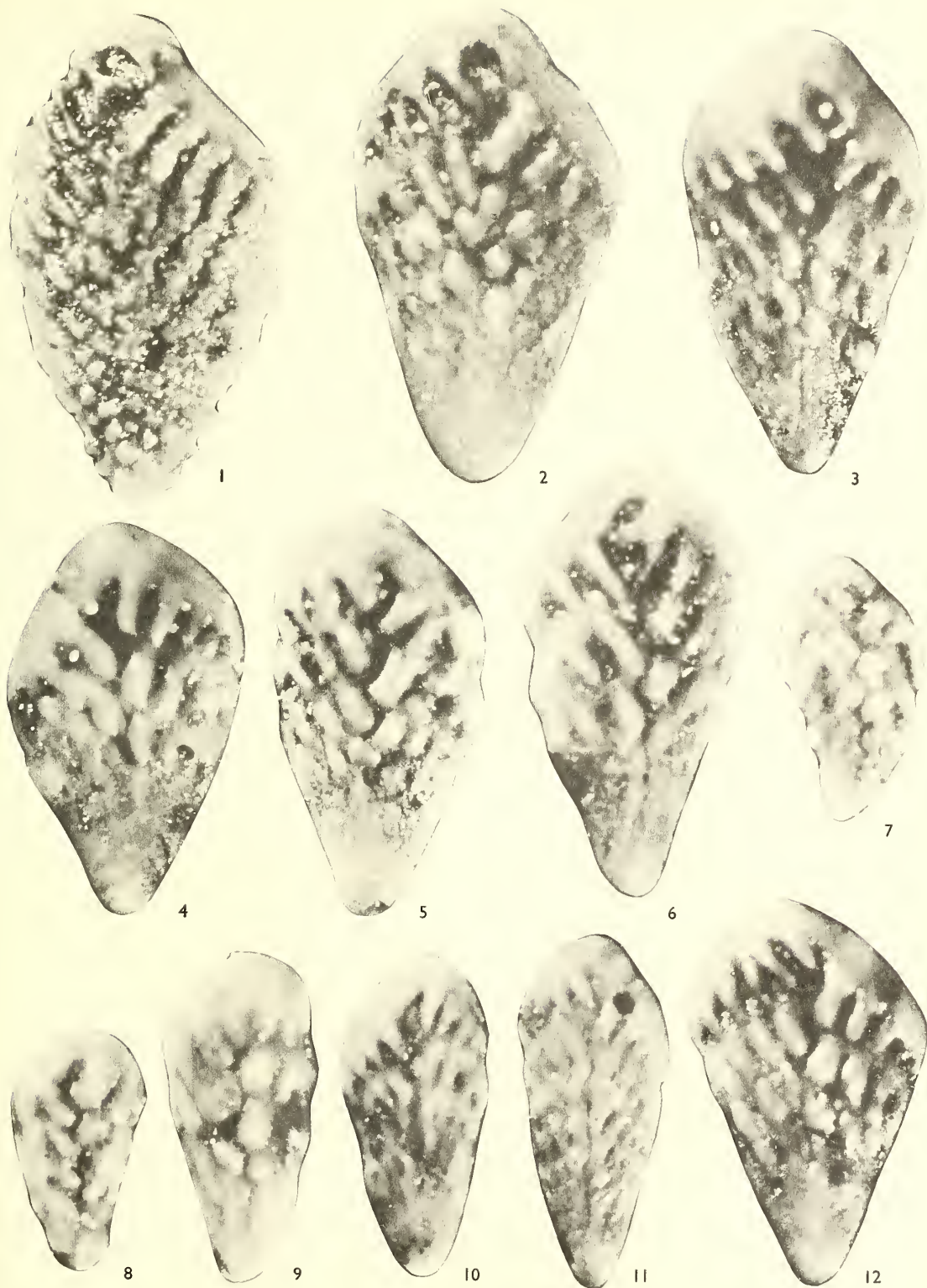
Fig. 1. *Bolivinoides australis* Edgell. $\times 118$. Topotype. C. Y. Creek, near Cardabia, on the west flank of Giralda Anticline, north-west Australia; Edgell's (1954) locality GC/304.

Figs. 2-6, 12. *Bolivinoides decorata* (Jones). $\times 118$. Showing variation in test shape and ornamentation. Upper Campanian, *Belemnitella mucronata* Zone. 2, Meudon, Paris Basin; BM P45711. 3-5, 12, Alum Bay, Isle of Wight, Sample A2, 405 ft. above base of *B. mucronata* Zone. 3, BM P45712; 4, BM P45713; 5, BM P45714; 12, BM P45716. 6, Culver Cliff, Isle of Wight, Sample C10; BM P45715.

Fig. 7. *Bolivinoides laevigata* Marie. $\times 118$. Upper Campanian, *Belemnitella mucronata* Zone, Culver Cliff, Isle of Wight; Sample C10, BM P45740.

Figs. 8, 9. *Bolivinoides strigillata* (Chapman). $\times 140$. Topotypes. Santonian, *Marsupites testudinarius* Zone, Phosphatic Chalk, Taplow, Buckinghamshire. 8, BM P45730; 9, BM P45731.

Figs. 10, 11. *Bolivinoides sidestrandensis* sp. nov. $\times 118$. Lower Maestrichtian, *Belemnitella lanceolata* Zone, Sidestrand, Norfolk. 10, Paratype, BM P45745; 11, Holotype, BM P45743.



(1948, p. 106, pl. 9, fig. 3) is located in the British Museum (Natural History). Barr and Cordey (1964, p. 308) examined the Williams-Mitchell collection and found this specimen to be clearly conspecific with *Bolivinoides decorata* (Jones). Williams-Mitchell (op. cit., pl. 10) lists the stratigraphical range of '*Bolivina strigillata*' (the only species in his paper referable to the genus *Bolivinoides*) as *Marsupites testudinarius* Zone to the top of the *Belemnitella mucronata* Zone in the Upper Cretaceous strata of England. This range undoubtedly represents the combined stratigraphical occurrence of several species of *Bolivinoides*.

Occurrence. The type locality of *Bolivinoides strigillata* is a small chalk pit, Lodge Pit, on the outskirts of Taplow, Buckinghamshire. Chapman obtained his specimens from about the middle of the phosphatic band in this pit. Osborne White and Treacher (1905) placed this part of the section in the *M. testudinarius* Zone (Santonian). *B. strigillata* appears to be restricted to the *M. testudinarius* Zone in England, but may possibly occur also in the *Offaster pilula* Zone.

Edgell (1954, pp. 70, 71) recorded *B. strigillata* from the Santonian of north-western Australia. Vassilenko (1961, p. 188, 297) reported this species from the Santonian and basal Campanian of the Soviet Union.

Hiltermann (1963, p. 205) and Hiltermann and Koch (1960, p. 71) listed the stratigraphic range of *B. strigillata* in north-western Europe as Upper Santonian to Lower Campanian. This range does not agree exactly with the range observed by me for this species in England. The apparent difference in range for this species between Germany and England may be due to the following reasons:

1. The *M. testudinarius* Zone is usually considered by British stratigraphers as Lower Santonian (Barnard and Banner 1953; Curry 1962), whereas many continental stratigraphers (Gignoux 1955, p. 392) place this zone in the Middle or Upper Santonian and regard the underlying *Micraster cor-anguinum* Zone as the Lower Santonian.

2. Many specimens which were once grouped with *B. strigillata*, or considered to be transition forms between *B. strigillata* and *B. decorata*, are now placed in the newly erected species *B. hiltermanni*. Probably most of the specimens referred to *B. strigillata* from the Lower Campanian (*Actinocamax quadratus* Zone) should now be considered as *B. hiltermanni*.

Bolivinoides hiltermanni sp. nov.

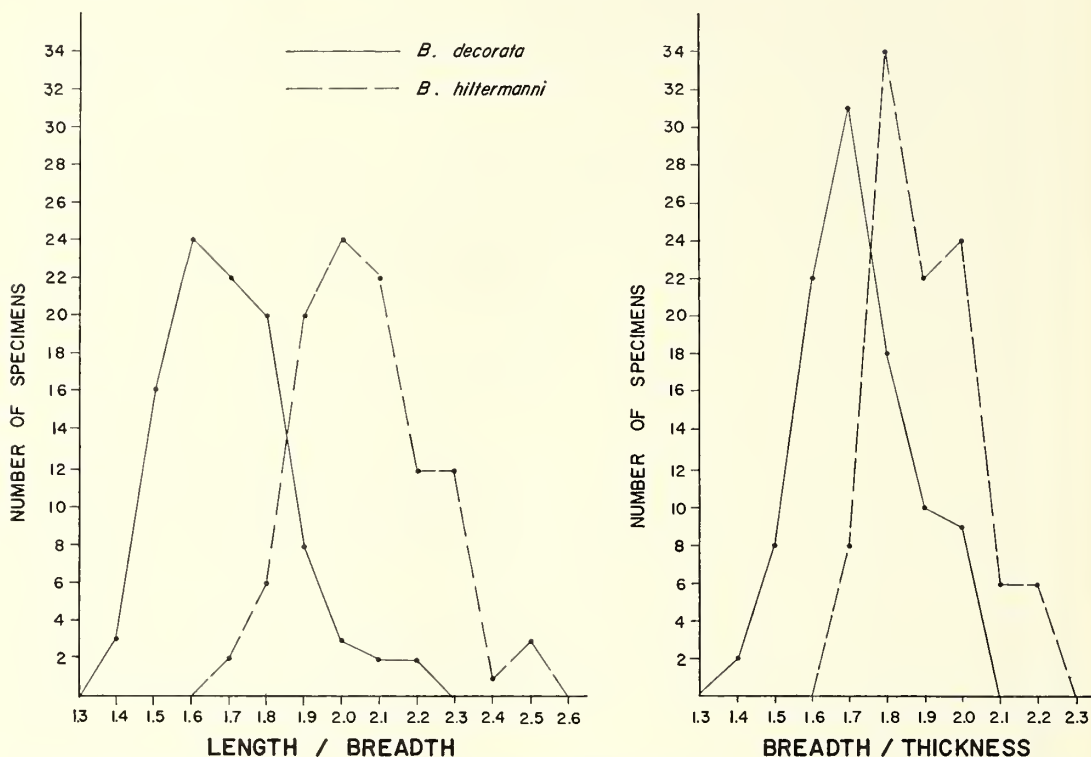
Plate 36, figs. 7, 8; Plate 37, figs. 1-3

Bolivinoides decorata (Jones) cf. *delicatula* Cushman; Edgell 1954, p. 71, pl. 13, fig. 7; pl. 14, fig. 7.

Bolivinoides sp. [transition form between *B. strigillata* (Chapman) and *B. decorata* (Jones)]; Hiltermann 1963, p. 209, pl. 1, figs. 2, 3, 7-9.

Description. Test completely biserial, elongate, tapering, greatest breadth and thickness near apertural end, initial end acutely rounded, apertural end more broadly rounded, elliptical in cross section; proloculus globular, succeeded by 7 to 8 pairs of tapering chambers uniformly and fairly rapidly increasing in size; sutures oblique, slightly curved, partially obscured by ornamentation; aperture a slit-like or loop-shaped opening located near centre of apertural face, sometimes bordered by weakly raised indistinct

lip, and with internal bolivine tooth plate structure; 2 to 4, usually 3 distinct lobes on final 2 or 3 pairs of chambers running perpendicular to sutures, less distinct lobes and knobs present on earlier chambers and usually surface of earliest 1 to 3 pairs of chambers



TEXT-FIG. 6. Diagrams showing comparison of length/breadth and breadth/thickness ratios of 100 specimens of *Bolivinooides decorata* (Jones) and 100 specimens of *B. hiltermanni* sp. nov. All specimens of *B. decorata* are from sample C10, *Belemnitella mucronata* Zone, Culver Cliff. All specimens of *B. hiltermanni* are from sample C29, *Actinocamax quadratus* Zone, Culver Cliff.

smooth; internal surface of chamber walls contains semi-conical knobs along top of suture, corresponding to depressed areas between lobes on external surface; proloculus smooth; wall very finely perforate; length/breadth ratio 1.7 to 2.5, most commonly

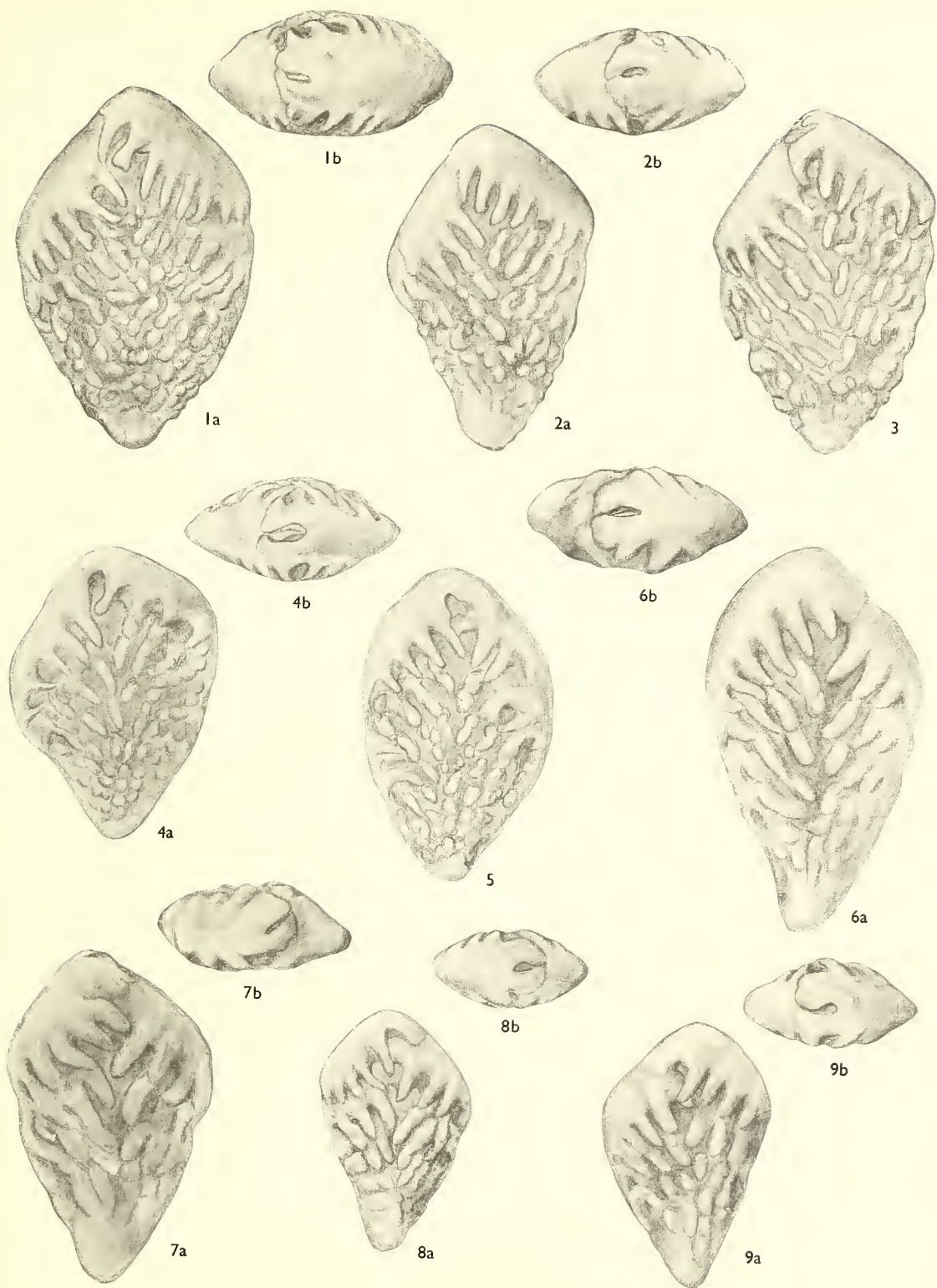
EXPLANATION OF PLATE 35

All illustrations shaded camera lucida drawings. *a* = side view; *b* = terminal view.

Figs. 1-3. *Bolivinooides australis* Edgell. $\times 90$. Topotypes. C. Y. Creek, near Cardabia, on the west flank of Giralia Anticline, north-west Australia; Edgell's (1954) locality GC/304.

Figs. 4, 5. *Bolivinooides miliaris* Hiltermann and Koch. $\times 95$. Ballycastle Pellet Chalk, west side Ballycastle Harbour, Northern Ireland. 4, BM P45722; 5, BM P45723.

Figs. 6-9. *Bolivinooides decorata* (Jones). $\times 95$. Upper Campanian, *Belemnitella mucronata* Zone. 6, 7, Culver Cliff, Isle of Wight, Sample C10; BM P45718, P45719. 8, Leicester Lime Co. Quarry, Drayton, Norfolk; BM P45717. 9, Alum Bay, Isle of Wight, 405 ft. above base of *B. mucronata* Zone, Sample A2; BM P45720.



BARR, Upper Cretaceous *Bolivinoides*

1.9 to 2.3; breadth/thickness ratio 1.7 to 2.2; approximate average length of adult specimen 0.50 mm.

Dimensions of holotype (BM P45724). Length 0.55 mm.; maximum breadth 0.25 mm.; maximum thickness 0.14 mm.

Remarks. *B. hiltermanni* represents the transition form between *B. strigillata* (Chapman) and *B. decorata* (Jones). Nevertheless, *B. hiltermanni* is quite distinct from both of these species; its lower boundary with *B. strigillata* and its upper boundary with *B. decorata* are usually sharply defined, and the transition between species takes place over a relatively short stratigraphic interval. *B. hiltermanni* is distinguished from *B. strigillata* by its: (1) larger size; (2) more elliptical cross section; (3) more rapidly tapering test; (4) more broadly rounded apertural end; and (5) usually having more ornamental lobes on its final chambers. *B. hiltermanni* differs from *B. decorata* by its: (1) smaller size; (2) less flaring test; (3) larger length/breadth ratio (usually 1.9 to 2.3 compared with 1.5 to 1.8 most usual for *B. decorata*, see text-fig. 6); (4) less distinct ornamentation, especially on the early part of the test; and (5) fewer ornamental lobes on the final chambers (most often 3 compared with the usual 4 or 5 for *B. decorata*).

B. hiltermanni is also closely related to *B. pustulata* Reiss, but is usually larger and has a more elliptical, less compressed end view. Furthermore, the ornamentation of *B. pustulata* is not as strongly developed and tends to be restricted to the medial part of the test. In the upper part of the *Actinocamax quadratus* Zone (upper part of the Lower Campanian) variants of *B. hiltermanni* become quite similar to Reiss's species. It is suggested that *B. hiltermanni* gave rise to *B. pustulata* during the middle part of the *A. quadratus* Zone. *B. hiltermanni* continued until the base of the *B. mucronata* Zone, at which time it gave rise to *B. decorata*, whereas *B. pustulata* gave rise to the *B. praelaevigata*–*laevigata* lineage near the beginning of the Upper Campanian.

B. hiltermanni is named in honour of Dr. Heinrich Hiltermann of Hannover, in recognition of his work on the genus *Bolivinoides*.

Occurrence. *B. hiltermanni* occurs in abundance throughout the *A. quadratus* Zone and more rarely in the *O. pilula* Zone in southern England. Although this species is found in abundance in the uppermost *A. quadratus* Zone, it does not survive into the *B. mucronata* Zone. The *A. quadratus* Zone–*B. mucronata* Zone (Lower Campanian–Upper Campanian) contact in southern England can be located with some accuracy at the stratigraphic position where *B. hiltermanni* is replaced by *B. decorata* (*s.s.*).

Bolivinoides decorata (Jones)

Plate 34, figs. 2–6, 12; Plate 35, figs. 6–9; Plate 36, figs. 1–5

Bolivina decorata Jones (in Wright 1875), pp. 87, 96, 97 (list only).

Bolivina decorata Jones (in Wright 1886), p. 330, pl. 27, figs. 7, 8.

Bolivina decorata Jones; Heron-Allen and Earland 1910, pl. 7, figs. 1, 2.

Bolivina decorata Jones; Macfadyen 1932, pl. 35, fig. 20.

Bolivinoides decorata (Jones); Dain 1934, pp. 33, 34, pl. 3, fig. 34.

Bolivinoides decorata (Jones); Marie 1941, p. 188, pl. 29, fig. 279.

Bolivina strigillata Chapman (*partim*); Williams-Mitchell 1948, p. 106, pl. 9, figs. 3a, b.

Bolivinoides decorata decorata (Jones); Hiltermann and Koch 1950, pp. 606–10, text-figs. 2–4, nos. 17–25, 27–31, 35–38, 42–45.

- Bolivinooides decorata decorata* (Jones); Hagn 1953, p. 74, pl. 6, fig. 22.
Bolivinooides decorata decorata (Jones); Reiss 1954, p. 155, pl. 28, figs. 5–8.
Bolivinooides decorata decorata (Jones); Hiltermann and Koch 1955, p. 365, pl. 28, fig. 4.
Bolivinooides decoratus decoratus (Jones); McGugan 1957, p. 339, pl. 32, figs. 10–13, 15 (*non* fig. 14).
Bolivinooides decorata decorata (Jones); Bieda 1958, pp. 32, 33, text-figs. 6a–c.
Bolivinooides regularis Reiss; Bieda 1958, pp. 36–38, text-figs. 9a–c.
Bolivinooides decorata decorata (Jones); Witwicka 1958, pp. 198, 199, pl. 9, figs. 9a, b.
Bolivinooides decoratus decorata (Jones); Bykova 1959, table 1, fig. 2.
Bolivinooides decoratus (Jones); Akimets 1961, pp. 188, 189, pl. 18, figs. 17, 18.
Bolivinooides decoratus decorata (Jones); Vassilenko 1961, pp. 189–90, pl. 39, figs. 8–10.
Bolivinooides decoratus decoratus (Jones); Hiltermann and Koch 1962, p. 315, table 19, pl. 46, fig. 7.
Bolivinooides decoratus (Jones); Kaptarenko-Chernousova *et al.* 1963, p. 111, pl. 25, fig. 4.

Description. Test biserial, pear-shaped in outline, elliptical in cross section; proloculus globular, succeeded by 8 to 9 pairs of slightly inflated, tapering chambers uniformly and rapidly increasing in size; sutures oblique, slightly curved, mostly obscured by ornamentation; aperture a slit-like or loop-shaped opening located near centre of apertural face, sometimes bordered by slightly raised lip and with internal tooth plate structure; 3 to 6 thick distinct lobes on final chamber running perpendicular to sutures, lobes on inner portion of chambers slightly thicker and more distinct than outer lobes, sometimes giving suggestion of 2 weakly defined medial ribs, ornamentation on earliest 1 to 3 pairs of chambers less distinct consisting of weakly raised lobes or knobs, often surface of earliest chambers smooth; proloculus smooth; wall calcareous, finely perforate; length/breadth ratio 1.4 to 2.2, most commonly 1.5 to 1.8; breadth/thickness ratio 1.4 to 2.0, most commonly 1.6 to 1.9; approximate average length of adult specimen 0.58 mm.

Dimensions of lectotype. Length 0.53 mm.; maximum breadth 0.34 mm.; maximum thickness 0.17 mm.

Remarks. In a short paper on some Upper Cretaceous Foraminifera collected from the chalk at Keady Hill, County Derry, Northern Ireland, Wright (1886, p. 330, pl. 27, figs. 7, 8) published the original description and illustrations of *Bolivina decorata*. However, this name had been used previously by T. Rupert Jones in unpublished work, and therefore Wright credited Jones with authorship of *Bolivina decorata*, even though this species was originally described in Wright's paper from material collected by Wright.

In Wright's collection of Foraminifera located in the museum of the Zoology Department, The Queen's University, Belfast, Northern Ireland, there is a small circular pillbox,

EXPLANATION OF PLATE 36

All illustrations shaded camera lucida drawings. *a* = side view; *b* = terminal view.

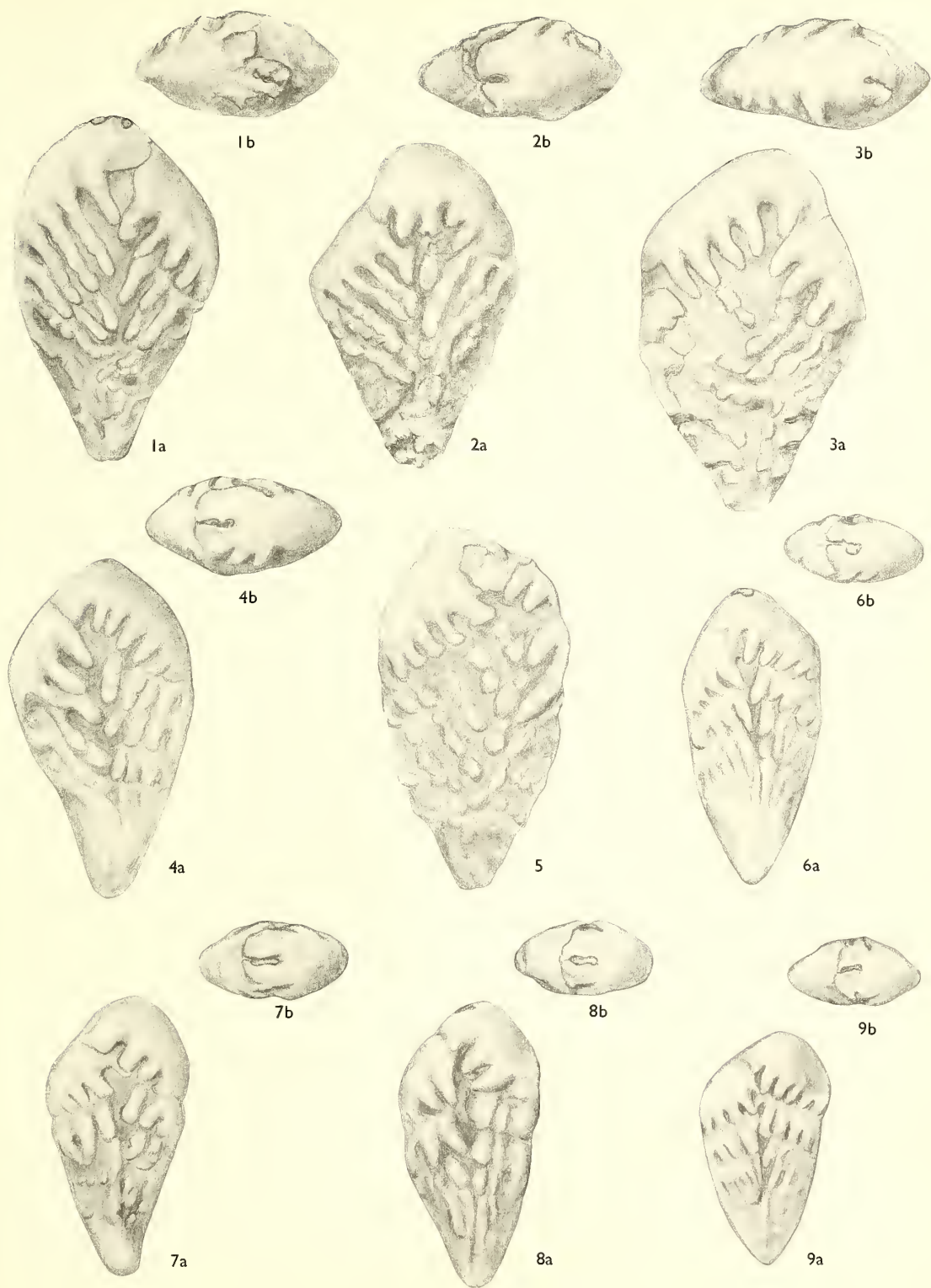
Figs. 1–3, 5. *Bolivinooides decorata* (Jones). $\times 100$. Syntypic specimens from Joseph Wright Collection.

1, Lectotype. 3, 5, Specimens with badly worn surface. Upper Campanian, *Belemnitella mucronata* Zone, Keady Hill, County Derry, Northern Ireland.

Fig. 4. *Bolivinooides decorata* (Jones). $\times 90$. Upper Campanian, *B. mucronata* Zone, Culver Cliff, Isle of Wight, Sample C10; BM P45721.

Figs. 6, 9. *Bolivinooides sidestrandensis* sp. nov. $\times 95$. Paratypes. Lower Maestrichtian, *Belemnitella lanceolata* Zone, Sidestrand, Norfolk. 6, BM P45744; 9, BM P45746.

Figs. 7, 8. *Bolivinooides hiltermanni* sp. nov. $\times 95$. Paratypes. Lower Campanian, *Actinocamax quadratus* Zone, Culver Cliff, Isle of Wight. 7, Sample C28, BM P45727; 8, Sample C29, BM P45726.



with celluloid cover, containing nine specimens of *Bolivinoides*, and is labelled as follows: *Bolivina decorata*, Chalk powder, Keady Hill, Co. Derry 109.

No other specimens of *Bolivinoides decorata* have been found which might be regarded as primary type material for this species. These specimens from the Wright Collection are probably those originally described as *Bolivina decorata* Jones and are here regarded as syntypes. Six of these specimens are broken or badly damaged and the remaining three specimens are worn to varying degrees. Nevertheless, several of these specimens are well enough preserved to show the morphology necessary in understanding the species. A single specimen which appears to be very similar to Wright's original illustration has been isolated from the syntypic series and is designated the *lectotype* of *Bolivina decorata* (here figured Pl. 36, figs. 1a, b). Three other specimens from this syntypic series are also illustrated (Pl. 36, figs. 2, 3, 5).



Edgell (1954, pp. 71, 72) described a new subspecies of *Bolivinoides* from Australia which he named *B. decorata* (Jones) *australis*. It is distinguished from *B. decorata* (s.s.) by: (1) having a smaller length/breadth ratio; (2) having more ornamental lobes on the final chambers (5–7 on the final chamber compared with 3–6 for *B. decorata* s.s.); (3) possibly being more commonly ornamented near its initial end; and (4) sometimes having a more rhomboidal outline.

Ten topotypic specimens of *B. decorata australis* from C. Y. Creek, west flank of Giralia Anticline, north-west Australia, have been kindly loaned to me for examination by N. H. Fischer, Bureau of Mineral Resources, Canberra, Australia. Four of these specimens are here illustrated for comparison with *B. decorata* s.s. (Pl. 34, fig. 1; Pl. 35, figs. 1–3). These specimens show *B. decorata australis* to be quite distinct from *B. decorata* s.s. and to be closer morphologically to *B. gigantea* Hiltermann and Koch. Possibly *B. australis* might best be considered a subspecies of *B. gigantea* or even synonymous with this species. Nevertheless, although it may be difficult to consistently distinguish *B. decorata australis* from *B. gigantea*, it appears to represent a transitional form between *B. decorata* and *B. gigantea*.

The evolution of *B. decorata* to *B. australis* takes place in Western Europe and North Africa in the earliest Maestrichtian (at the beginning of the *Belennitella lanceolata* Zone). Specimens of *B. decorata* become increasingly similar to *B. australis* in latest Campanian times. The type specimens of *B. decorata* from Keady Hill are probably from the upper part of the *B. mucronata* Zone and, consequently, two or three of the specimens of *B. decorata* from the Wright Collection represent rather advanced forms of this species.

Specimens referred to *Bolivina decorata* Jones by Heron-Allen and Earland (1910, p. 409, pl. 7, figs. 1, 2) are located in the British Museum (Natural History). These specimens have been re-examined and were found to be clearly conspecific with the type for *Bolivinoides decorata*. These specimens are from chalk meal from the interior of a cavernous flint nodule found on the beach at Selsey Bill, Sussex. The presence of *B. decorata* in the fauna from this flint nodule would strongly suggest that the nodule was originally from the *B. mucronata* Zone.

TEXT-FIG. 7. Terminal view of small specimen of *Bolivinoides decorata* (Jones) with final chamber mostly broken away exposing corrugated nature of lower part of chamber wall. This view shows that the external 'ornamental' lobes are formed by folds in the chamber wall rather than by a thickening of the test wall.

Occurrence. *B. decorata* occurs in abundance throughout the *B. mucronata* Zone in southern England and appears to be restricted to this zone. The type locality for *B. decorata* is at Keady Hill, County Derry, Northern Ireland, which is probably in the upper part of the *B. mucronata* Zone. Wright (1875, pp. 96, 97) also recorded this species from a number of other Upper Cretaceous localities in Northern Ireland.

McGugan (1957, p. 339, pl. 32, figs. 10–15) recorded *B. decorata* from the Ballycastle Pellet Chalk of Northern Ireland. R. E. H. Reid, Queen's University, Belfast, has kindly sent me material from the Ballycastle Pellet Chalk from the main exposure on the west side of Ballycastle Harbour. This material contained a number of specimens of *B. decorata* along with rarer specimens of *B. sidestrandensis* sp. nov. and *B. miliaris* Hiltermann and Koch. All specimens of *Bolivinoidea* from this material were worn to varying degrees. The benthonic fauna contained a mixture of Campanian and Maestrichtian species and represents largely, if not entirely, a derived fauna. McGugan (op. cit., p. 33) stated that the character of the exposures of the Ballycastle Pellet Chalk suggested deposition of this formation in some kind of channel in the top of the underlying Upper Cretaceous Chalk. R. E. H. Reid informs me that the principal exposure of the Ballycastle Pellet Chalk contains blocks of Tertiary basalt. It appears that the Ballycastle Pellet Chalk was derived by Tertiary erosion of an Upper Cretaceous surface (cf. Charlesworth 1963, p. 369) and the specimens of *Bolivinoidea* found in this formation have also been derived from this nearby Upper Cretaceous Chalk.

I have found *B. decorata* in the newly discovered Ballydeenlea Chalk of County Kerry, Ireland (Walsh 1960). The presence of this species along with the rest of the fauna indicates that the Ballydeenlea Chalk is Campanian in age, not Middle Chalk (Turonian), as had previously been suggested (Walsh 1960, p. 113). A description of the foraminiferal fauna from this formation will soon be published.

Marie (1941, p. 188) recorded *B. decorata* from the *B. mucronata* Zone of the Paris Basin. I have also found abundant specimens of *B. decorata* in the upper *B. mucronata* Zone at Meudon, on the outskirts of Paris. These specimens are 10 to 15 per cent larger than the average from England, but are very similar in all other characteristics.

I have found specimens of *B. decorata* in an advanced stage of development in material from R. K. Olsson's (1964, p. 160) locality NJK 134 in the Marshalltown Formation of New Jersey. Olsson (op. cit., p. 163) recorded *Globotruncana calcarata* Cushman, usually regarded as a reliable index fossil to the Upper Campanian, from this same locality.

Bolivinoidea miliaris Hiltermann and Koch

Plate 35, figs. 4, 5

Bolivinoidea draco (Marsson) *miliaris* Hiltermann and Koch 1950, pp. 604–6, text-figs. 2–4, nos. 32–34 (?), 39–41, 46–48; text-fig. 5, nos. 39a–c.

Bolivinoidea draco miliaris Hiltermann and Koch; Reiss 1954, p. 155, pl. 28, figs. 9–12, 14.

Bolivinoidea draco miliaris Hiltermann and Koch; Pożaryska 1954, p. 254, text-fig. 4.

Bolivinoidea miliaris Hiltermann and Koch; Hofker 1957, p. 267, text-fig. 322b.

Bolivinoidea draco miliaris Hiltermann and Koch; Bieda 1958, pp. 44, 45, figs. 14a–c.

Bolivinoidea draco miliaris Hiltermann and Koch; Hiltermann and Koch 1960, p. 72.

Bolivinoidea miliaris Hiltermann and Koch; Vassilenko 1961, pp. 200, 201, pl. 40, figs. 4a–c, pl. 41, figs. 1a–c.

Bolivinoidea draco miliaris Hiltermann and Koch; Hiltermann and Koch 1962, p. 317, table 19, pl. 46, fig. 9.

Bolivinoides draco miliaris Hiltermann and Koch; Hiltermann 1963, p. 222, pl. 4, figs. 21–23.

Bolivinoides draco miliaris Hiltermann and Koch; van Hinte 1963, pp. 106, 107, pl. 13, figs. 7, 8.

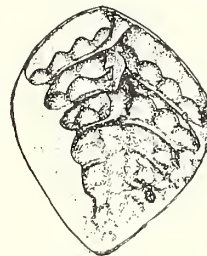
Remarks. *B. miliaris* is morphologically similar to *B. decorata* (Jones) in many respects and appears to have been derived from the latter during the late *B. mucronata* Zone (uppermost Campanian). *B. miliaris* can be distinguished from *B. decorata* by having a smaller length/breadth ratio. Its lateral outline is more rhomboidal than the more elongate, pear-shaped outline of *B. decorata*; the maximum breadth of *B. miliaris* is nearer the mid point of test, whereas the maximum breadth of *B. decorata* is closer to the apertural end. The ornamentation on *B. miliaris* is usually less regular than that of *B. decorata* and often, on the earliest 30 to 50 per cent of the test, the ornamentation consists of small knobs. The earliest 1 to 3 pairs of chambers of *B. decorata* are ornamented by less distinct lobes or knobs, or more often, these early chambers have a smooth surface.

B. miliaris differs from *B. australis* Edgell by having fewer ornamental lobes on its final chambers. *B. miliaris* usually has 4 and sometimes 5, whereas *B. australis* has 5 to 7 on its latest chambers. *B. miliaris* has a smaller size and usually has a more rhomboidal outline, although variants of *B. australis* sometimes possess a similar rhomboidal outline.

B. miliaris gave rise to *B. draco* (Marsson) during the upper part of the Lower Maestrichtian. The earliest 50 to 60 per cent of the test of *B. draco* is more flaring than that of *B. miliaris*, which has a less angular outline. *B. draco* also has two very distinctive, well-developed, parallel medial ribs, which are produced by the fusing of the inner 'ornamental' lobes. Hiltermann and Koch (1960, p. 73) listed the stratigraphic range of *B. draco* in north-west Europe as the upper part of the Lower Maestrichtian to the top of the Maestrichtian. I have observed the same range for this species in western Europe and North Africa; however, I have not found *B. draco* in the British Isles. McGugan (1957, pl. 32, fig. 17) illustrated a specimen from the Ballycastle Pellet Chalk of Northern Ireland which he referred to *B. draco draco* Hiltermann and Koch. It is poorly preserved and there is some doubt as to whether this specimen should be considered *B. draco* (*s.s.*). Curry (1962, p. 180) also recorded a single specimen which he referred to *Bolivinoides* cf. *draco* from a submarine core from the English Channel.

Occurrence. Rare specimens of *B. miliaris* were found in the Ballycastle Pellet Chalk along the west side of Ballycastle Harbour, Northern Ireland. Curry (1962, p. 182, 184) recorded *B. miliaris* from two submarine cores which were obtained from an area in the English Channel halfway between the Isle of Wight and Cherbourg. The Upper Cretaceous fauna of the Ballycastle Pellet Chalk, which consists of a mixture of late Campanian and early Maestrichtian foraminifera, appears to be a derived fauna (see remarks under *B. decorata*) and therefore the age of these specimens is not precisely known.

The holotype of *B. miliaris* is from a bore hole near Niemburg, north-west Germany, and is from the *B. mucronata* Zone. Hiltermann (1963, p. 205) and Hiltermann and Koch (1960, p. 72) listed the range of *B. miliaris* in north-west Europe as uppermost Campanian and Lower Maestrichtian.



TEXT-FIG. 8. Bisected specimen of *Bolivinoides draco* (Marsson) showing tooth plate structure and internal semi-conical bulges along base of chambers, corresponding to depressed areas between lobes on external surface.

Bolivinooides pustulata Reiss

Plate 37, figs. 4a, b

Bolivinooides pustulata Reiss 1954, p. 156, pl. 29, figs. 9, 10.*Bolivinooides granulata* Hofker 1957, pp. 250, 251, text-figs. 303, 310.*Bolivinooides pustulata* Reiss; Hiltermann 1963, p. 214, pl. 2, fig. 17.*Bolivinooides granulata* Hofker; Hiltermann 1963, p. 213, pl. 2, figs. 5, 11, 12.

Remarks. Topotypic specimens of *B. pustulata* have been compared with specimens from southern England and they appear to be conspecific. *B. pustulata* is closely related to *B. hiltermanni* (see p. 231) and it is suggested that the latter is the ancestral species. It has a much greater stratigraphic range than *B. pustulata*, which is restricted to the upper part of the *A. quadratus* Zone.

B. pustulata appears to be the direct ancestor of *B. praelaevigata* sp. nov., which is distinguished from it by its smaller, more compressed, more gradually tapering test. The ornamentation of *B. praelaevigata* is also more weakly developed and even more restricted to the medial portion of the test than that of *B. pustulata*.

B. pustulata is morphologically very similar to *B. granulata* Hofker and the latter is tentatively regarded as a junior synonym of *B. pustulata*. Unfortunately, however, the original illustrations given by Hofker (1957, text-figs. 303–10) do not allow a very exact comparison of all features and I have been unable to examine type material of *B. granulata*. Final judgement on this point must be withheld until type material can be studied.

EXPLANATION OF PLATE 37

All illustrations shaded camera lucida drawings, $\times 140$. *a* = side view; *b* = terminal view.

Figs. 1–3. *Bolivinooides hiltermanni* sp. nov. Lower Campanian, *Actinocamax quadratus* Zone, Culver Cliff, Isle of Wight. 1, Holotype, Sample C29, BM P45724. 2, Paratype, Sample C24. 3, Paratype, Sample C29, BM P45725.

Fig. 4. *Bolivinooides pustulata* Reiss. Lower Campanian, *A. quadratus* Zone, Culver Cliff, Isle of Wight; Sample 23, BM P45741.

Fig. 5. *Bolivinooides* aff. *B. hiltermanni* sp. nov. Transitional form between *B. pustulata* and *B. hiltermanni*. Lower Campanian, *A. quadratus* Zone, Culver Cliff, Isle of Wight; Sample C23, BM P45728.

Fig. 6. *Bolivinooides sidestrandensis* sp. nov. Paratype, BM P45745. Lower Maestrichtian, *Belemnitella lanceolata* Zone, Sidestrand, Norfolk.

Figs. 7–9. *Bolivinooides strigillata* (Chapman). Topotypes. Santonian, *M. testudinarius* Zone, Phosphatic Chalk, Taplow, Buckinghamshire. Specimens 7 and 8 are also illustrated by unretouched photographs on Plate 34. 7, BM P45729; 8, BM P45730; 9, BM P45731.

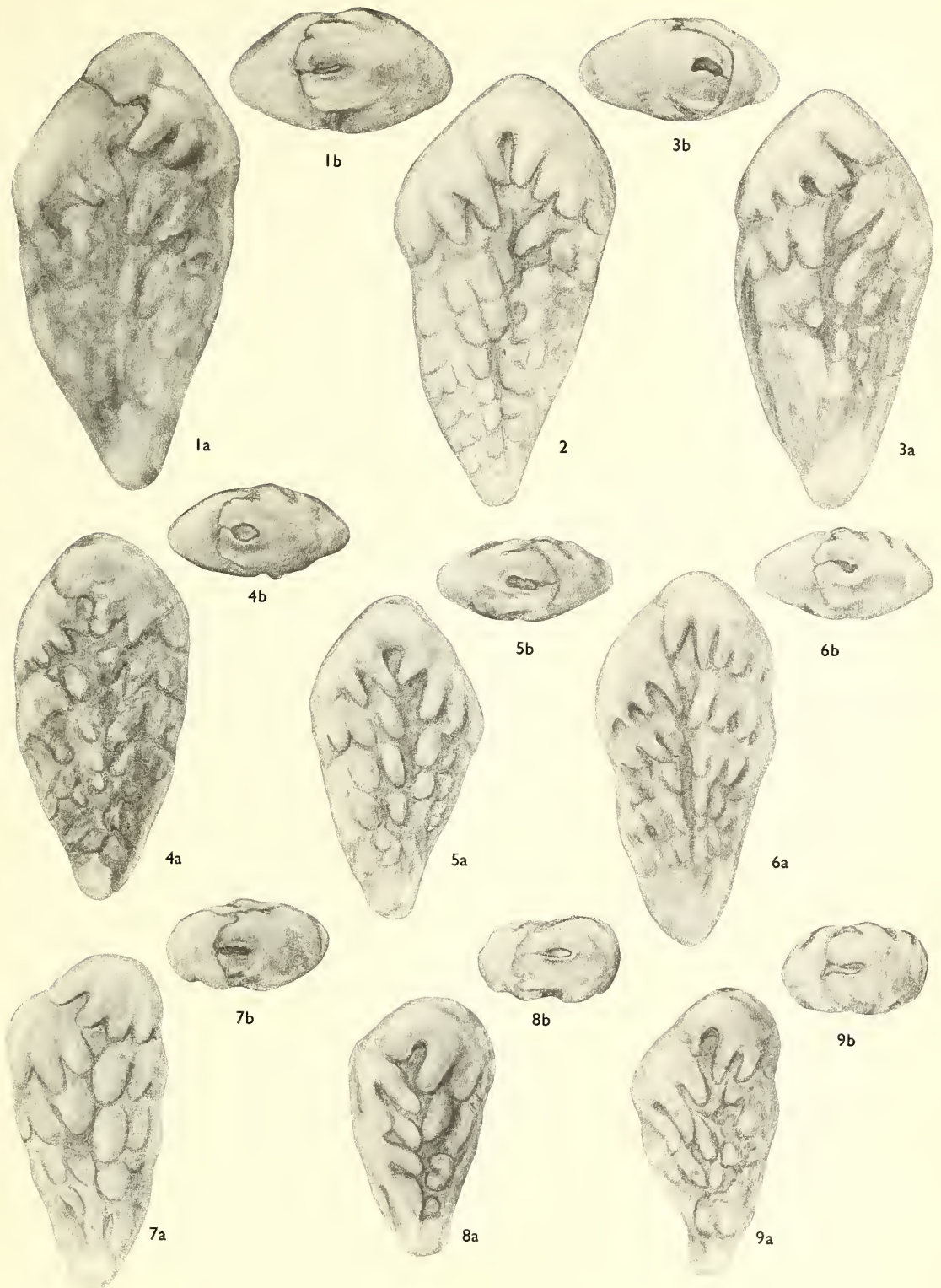
EXPLANATION OF PLATE 38

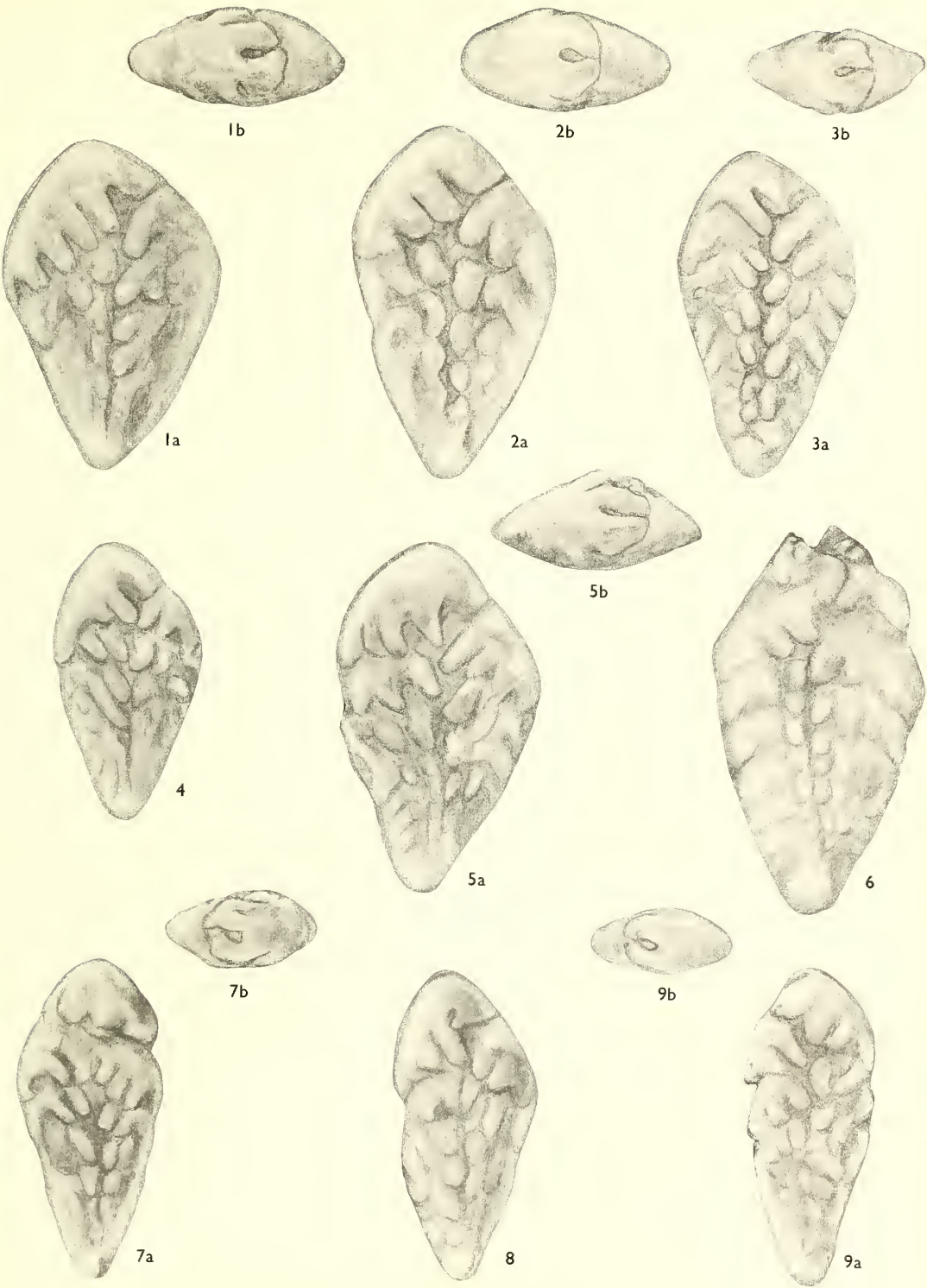
All illustrations shaded camera lucida drawings, $\times 140$. *a* = side view; *b* = terminal view.

Figs. 1–5. *Bolivinooides laevigata* Marie. Series of specimens showing variation in test shape and ornamentation. 1, 5, Lower Maestrichtian, *B. lanceolata* Zone, Sidestrand, Norfolk. 2–4, Upper Campanian, *B. mucronata* Zone, Culver Cliff, Isle of Wight, Sample C10. 1, BM P45735; 2, BM P45736; 3, BM P45737; 4, BM P45738; 5, BM P45739.

Fig. 6. *Bolivinooides peterssoni* Brotzen. Final chamber broken. Lower Maestrichtian, *B. lanceolata* Zone, Sidestrand, Norfolk; BM P45742.

Figs. 7–9. *Bolivinooides praelaevigata* sp. nov. Lower part of Upper Campanian, *B. mucronata* Zone, Culver Cliff, Isle of Wight. 7, Holotype, Sample C13, BM P45732; 8, Paratype, Sample C13, BM P45734; 9, Paratype, Sample C18, BM P45733.





Occurrence. *B. pustulata* is restricted to the upper part of the *A. quadratus* Zone (upper part of the Lower Campanian). Reiss (1954, text-fig.1) listed an identical range for this species.

Bolivinoides praelaevigata sp. nov.

Plate 38, figs. 7–9

Description. Test biserial, elongate, very gradually tapering, greatest breadth near apertural end, flatly elliptical in cross section; proloculus smooth, globular, succeeded by 7 or 8 pairs of slightly inflated, tapering chambers, uniformly and fairly rapidly increasing in size; sutures oblique, slightly curved, apparent in peripheral portion of test, obscured by ornamentation in medial area; aperture a slit-like or small loop-shaped opening located near centre of apertural face, bordered by weakly raised lip and with internal tooth plate structure; 2 or 3 weakly raised lobes on final chambers running perpendicular to sutures, ornamentation on earlier chambers less distinct consisting of 1 or 2 weakly raised lobes; lobes on inner portion of chambers slightly thicker and more apparent than outer lobes, sometimes giving appearance of 2 very weakly defined medial ribs; wall calcareous, finely perforate; length/breadth ratio 1.9 to 2.5, most commonly 2.0 to 2.3; breadth/thickness ratio 2.0 to 2.6; approximate average length of adult specimen 0.35 mm.

Dimensions of holotype (BM P45732). Length 0.36 mm.; breadth 0.17 mm.; thickness 0.07 mm.

Remarks. *B. praelaevigata* is the direct ancestral species of *B. laevigata* Marie. It occurs in the lower *B. mucronata* Zone and gives rise to *B. laevigata* in about the middle part of this zone. No specimens of *B. laevigata* were found in the basal *B. mucronata* Zone although *B. praelaevigata* was common. In the middle part of this zone, however, a complete gradation was observed between *B. praelaevigata* and *B. laevigata*. The length/breadth ratio of *B. praelaevigata* is most commonly 2.0 to 2.3, whereas that of *B. laevigata* is usually 1.8 to 2.0. Furthermore, the test of *B. praelaevigata* has a smaller breadth, is more compressed and often slightly smaller. The ornamentation of both species, however, is quite similar.

Occurrence. *B. praelaevigata* is restricted to the lower part of the *B. mucronata* Zone and appears to be a useful index fossil for this part of the Campanian. *B. laevigata*, on the other hand, has a much greater stratigraphic range, extending into the Maestrichtian.

Bolivinoides laevigata Marie

Plate, 34, fig. 7; Plate 38, figs. 1–5

- Bolivinoides decorata* (Jones) *laevigata* Marie 1941, p. 189, pl. 29, fig. 281.
Bolivinoides decorata laevigata Marie; Hiltermann 1952, p. 63, text-figs. 4, 5.
Bolivinoides praecursor Reiss 1954, pp. 156, 157, pl. 30, figs. 4–8.
Bolivinoides sp., Reiss 1954, p. 157, pl. 29, fig. 11.
Bolivinoides laevigata Marie; Hiltermann and Koch 1955, pp. 367, 368, pl. 27, figs. 13–15.
Bolivinoides praecursor Reiss; Bieda 1958, pp. 41, 42, text-fig. 12.
Bolivinoides laevigata Marie; Hiltermann and Koch 1960, p. 72, table 3.
Bolivinoides laevigatus Marie, Hiltermann and Koch 1962, p. 316, table 19, pl. 51, fig. 10.
Bolivinoides laevigatus Marie; Hiltermann 1963, p. 213, pl. 2, figs. 6–10.

Description. Test biserial, gradually tapering, flatly elliptical cross section; proloculus smooth, globular, succeeded by 7 to 9 pairs of slightly inflated, tapering chambers uniformly and rapidly increasing in size; sutures oblique, slightly curved, apparent in peripheral portion of test, obscured by ornamentation in medial area; aperture a slit-like or small loop-shaped opening located near centre of apertural face bordered by weakly raised lip and with internal tooth plate structure; 2 to 4 weakly raised lobes present on final chambers near medial position of test, 1 or 2 lobes present on earlier chambers near medial part of test, lobes become progressively weaker toward periphery; wall calcareous, finely perforate; length/breadth ratio 1.5 to 2.1, most commonly 1.8 to 2.0; breadth/thickness ratio 1.8 to 2.4; approximate average length of adult specimen 0.40 mm.

Remarks. *B. laevigata* was originally described as a subspecies of *B. decorata* (Jones) (Marie 1941, p. 189). These species are quite distinct, however, and are not directly related. I agree with Reiss (1954, p. 157) and subsequent authors who have regarded these forms as separate species. *B. laevigata* is smaller, more compressed, and has much more weakly developed ornamentation than *B. decorata*.

Reiss (loc. cit.) did not recognize *B. laevigata* in the Middle East, but described a form which he believed closely related to this species and which he named *B. praecursor*. This species has a similar length/breadth ratio to that of *B. laevigata*, and the stratigraphic ranges of these two forms are identical. However, Reiss considered them distinct because of ornamental differences. Unfortunately, when Marie (1941, p. 189) originally described *B. laevigata* he illustrated only a single specimen and did not show or describe the variation in ornamentation for this species. After examination of numerous specimens of *B. laevigata* from the *B. mucronata* Zone of the Paris Basin and southern England, I believe that *B. praecursor* falls within the range of variation of *B. laevigata* and should be regarded as a junior synonym of that species.

B. laevigata is the direct ancestor of *B. peterssoni* Brotzen, giving rise to the latter during the early part of the Maestrichtian. Consequently, these species are very similar morphologically and are often difficult to distinguish consistently. *B. peterssoni* has more distinct sutures, shorter and sometimes fewer 'ornamental' lobes and is often less compressed than *B. laevigata*.

Occurrence. *B. laevigata* occurs in the *B. mucronata* Zone (Upper Campanian) of southern England and in the Lower Maestrichtian chalk at Sidestrand, Norfolk. This species was originally described from the *B. mucronata* Zone of the Paris Basin. Hiltermann and Koch (1960, p. 72) and Hiltermann (1963, p. 205) recorded the range of *B. laevigata* in north-west Europe as Upper Campanian and Lower Maestrichtian. Reiss (1954, p. 160) recorded a similar range for *B. praecursor*.

Bolivinoides peterssoni

Plate 38, fig. 6

Bolivinoides peterssoni Brotzen 1945, p. 49, pl. 1, fig. 10.

Bolivinoides peterssoni Brotzen; Pożaryska 1954, p. 256, text-fig. 8.

Bolivinoides peterssoni Brotzen; Reiss 1954, p. 157, pl. 30, figs. 12–14.

Bolivinoides peterssoni Brotzen; Hiltermann and Koch 1955, pp. 366, 367, pl. 28, figs. 7, 8.

Bolivinoides peterssoni Brotzen; Hiltermann and Koch 1960, p. 72, chart 3.

Bolivinooides peterssoni Brotzen; Vassilenko 1961, pp. 198, 199, pl. 40, figs. 8a, b.

Bolivinooides peterssoni Brotzen; Hiltermann and Koch 1962, p. 317, pl. 50, fig. 16.

Bolivinooides peterssoni Brotzen; Hiltermann 1963, p. 213, pl. 2, figs. 1–3.

Occurrence. A few specimens of *B. peterssoni* were found in the Lower Maestrichtian chalk at Sidestrand, Norfolk. Numerous specimens of this species were also found in the Upper Maestrichtian chalk at Stevns Klint, Denmark. This species ranges throughout almost the entire Maestrichtian, but appears to be most abundant in the upper part of this stage. The type specimens of *B. peterssoni* were originally described by Brotzen (1945, p. 49) from Upper Maestrichtian strata penetrated by a bore hole at Höllviken, Scania, Sweden.

Bolivinooides sidestrandensis sp. nov.

Plate 34, figs. 10, 11; Plate 36, figs. 6, 9; Plate 37, fig. 6

Bolivinooides decorata delicatula Cushman; Hiltermann and Koch 1950 (*non* Cushman 1927), p. 612, fig. 5, nos. 65–67.

Bolivinooides decorata delicatula Cushman; Hiltermann 1952, pp. 61, 63, text-figs. 4, 5.

Bolivinooides decorata delicatula Cushman; Pożaryska 1954, pp. 255, 256, text-fig. 7.

Bolivinooides decorata delicatula Cushman; Witwicka 1958, p. 199, pl. 9, figs. 10a, b.

Bolivinooides delicatula Cushman; Bieda 1958, pp. 38, 39, text-figs. 10a–c.

Bolivinooides decorata delicatula Cushman; Hiltermann 1960, p. 72, table 3.

Bolivinooides delicatulus Cushman; Vassilenko 1961, pp. 193–5, pl. 40, figs. 7a, b.

Bolivinooides decoratus delicatulus Cushman; Hiltermann and Koch 1962, p. 315, table 19, pl. 47, fig. 5.

Bolivinooides delicatulus regularis Reiss; Hiltermann 1963 (*non* Reiss 1954), p. 205, pl. 3, figs. 7, 11, 12.

Description. Test biserial, elongate, gradually tapering with greatest breadth near apertural end, flatly elliptical in cross section; proloculus smooth, globular, followed by 7 or 8 pairs of slightly inflated, tapering chambers uniformly and rapidly increasing in size; sutures oblique, slightly curved, usually obscured by ornamentation but sometimes fairly distinct in latest part of test; aperture a slit-like or small looped-shaped opening located near centre of apertural face, bordered by weakly raised lip and with internal tooth plate structure; 5 or 6 well-defined but small, uniformly arranged, ornamental lobes on final chambers running perpendicular to sutures, ornamentation on earlier chambers less distinct but arranged in same uniform manner; wall calcareous, finely perforate; length/breadth ratio 1·8 to 2·5; breadth/thickness ratio 2·1 to 2·8; approximate average length of adult specimen 0·45 mm.

Dimensions of holotype (BM P45743). Length 0·48 mm.; maximum breadth 0·20 mm.; maximum thickness 0·08 mm.

Remarks. Specimens which are now included in the species *B. sidestrandensis* have been commonly recorded from various parts of Europe. However, they have usually been considered to belong to either *B. delicatula* Cushman or *B. regularis* Reiss. Cushman (1927, p. 90) originally described *B. decorata* (Jones) var. *delicatula* from the Lower Tertiary Velasco Shale near Vera Cruz, Mexico. Later Cushman (1946, p. 113, pl. 48, figs. 10–14) recorded *B. decorata delicatula* from various formations of Navarro and Taylor ages from the Gulf Coastal Area of the U.S.A. Reiss (1954, p. 158) elevated Cushman's variety to specific rank as he found no evidence to support the contention

that *B. decorata delicatula* was derived from *B. decorata* (Jones) or even from the 'decorata' group. Furthermore, Reiss regarded the specimens identified by Cushman (loc. cit.) as *B. decorata delicatula* from formations of lower Navarro and Taylor ages as being distinct from the typical form. He therefore proposed the name *Bolivinoides regularis* for the Navarro-Taylor form, with a specimen figured by Cushman (1931, pl. 35, fig. 13; 1946, pl. 48, figs. 12a, b) from the Saratoga Chalk of Howard County, Arkansas, as the holotype. Reiss also concluded that the specimens figured as *B. decorata delicatula* Cushman by Hiltermann and Koch (1950) and Hiltermann (1952), although differing in some detail, were conspecific with his new species *B. regularis*.

I agree with Reiss that the specimens figured by Cushman (1946, pl. 48, figs. 10-14) as *B. decorata delicatula* represent two distinct species. Cushman's (op. cit., pl. 48, figs. 11, 12) specimens which Reiss placed in his species *B. regularis* are indeed very different from the Danian-Paleocene specimens of *B. delicatula*; however, they are quite similar to *B. decorata* (Jones). The holotype of *B. regularis*, which is located in the U.S. National Museum, Washington, D.C., has been examined and was found to have a greater relative thickness than was shown by Cushman's illustrations. The ornamentation has a somewhat more uniform or regular appearance than is usually exhibited by *B. decorata*, but in most respects it is very similar to this species. Only by the examination of additional topotypic specimens will one be able to decide with assurance whether *B. decorata* (Jones) and *B. regularis* Reiss are distinct or conspecific. It may be that *B. regularis* would best be considered a geographic subspecies of *B. decorata*; however, final judgement on this taxonomic problem must be withheld until additional material becomes available.

On the other hand, I do not concur with Reiss's contention that the specimens illustrated by Hiltermann and Koch (1950, p. 612, fig. 5, nos. 65-67) and Hiltermann (1952, pp. 61, 63, text-figs. 4, 5) from north-west Germany are conspecific with the holotype of *B. regularis* from the Saratoga Chalk of Arkansas. The specimens from Germany appear to be almost identical with the specimens from England which are placed in the new species *B. sidestrandensis*. The latter differs from *B. regularis* by having a smaller size, being more compressed, and having a less flaring test with a greater length/breadth ratio. *B. sidestrandensis* has the same general shape as *B. delicatula* (s.s.), but is distinguished by its characteristic ornamentation, which is much more distinct and uniform than that of *B. delicatula*.

Occurrence. *B. sidestrandensis* occurs in abundance in the Lower Maestrichtian chalk exposed in the seacliff section at Sidestrand, Norfolk. Black (1964) described some of the fossil nannoplankton from this locality. *B. sidestrandensis* was also found in the Ballycastle Pellet Chalk from the main exposure along the west side of Ballycastle Harbour, Northern Ireland. No specimens of this species were recovered from the *B. mucronata* Zone of southern England. However, Hiltermann (1963, p. 205) recorded the stratigraphic range of *B. delicatula regularis* (= *B. sidestrandensis*) as upper Upper Campanian to lower Upper Maestrichtian.

Dr. Max Meijer kindly provided me with material from the Lower Maestrichtian (*B. lanceolata* Zone) of Grindaal, north-east Belgium. This glauconitic chalk contained numerous specimens of *B. sidestrandensis* associated with rare specimens of *B. peterssoni* Brotzen and *B. australis* Edgell.

Hiltermann (1963, p. 217, pl. 3, fig. 11) illustrated a specimen identified as *B. delicatulus regularis* (Reiss) (= *B. sidestrandensis*) from the Marshalltown Formation of New Jersey. I have also found specimens of *B. sidestrandensis* in material from Olsson's (1964, p. 160) locality NKJ 134 in the Marshalltown Formation of New Jersey. This locality is probably uppermost Campanian in age.

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THE DEVONIAN BLASTOID *BELOCRINUS* FROM FRANCE

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ABSTRACT. The nature and validity of the Lower Devonian blastoid genus *Belocrinus* Munier-Chalmas from north-western France has been in doubt since its original description. A complete specimen of the type species, *B. cottaldi* (Munier-Chalmas) is described and illustrated. The genus *Belocrinus* is redefined; it is similar to, but not synonymous with, the genus *Cordyloblastus* Fay. The number of anal deltoids and hydrospires in *Belocrinus* could not be determined. The ontogenetic development of the plates of the calyx is also described.

IN 1876, Munier-Chalmas briefly described a peculiar fossil from the Lower Devonian of north-western France which he named *Beleunnocrinus cottaldi*. He believed that it was a crinoid, composed of five longitudinal pieces. Finding his generic name to be preoccupied, he proposed the name *Belocrinus* for it in 1881. The description was repeated by Oehlert (1882) and specimens were illustrated for the first time; in his plate legend (p. 363) he described the calyx as being composed of three pieces. Etheridge and Carpenter (1883) were the first workers to attribute this fossil to the Blastoidea. They called attention to Oehlert's figures and stated that they appeared to represent the elongated basal cup of a *Troosticrinus* or *Pentremitidea* (p. 245). Munier-Chalmas furnished them with a specimen which they described and illustrated in 1886; they diagnosed the material as the large basal plates of a *Metablastus*. No additional material other than the basals was known until Phillipot (1957) described a complete specimen which was in the H. de Keravel collection at the Université de Rennes. His description furnished the first detailed information about the radials, deltoids, and ambulacra. Unfortunately, the summit was obscured by matrix. On the basis of the available evidence, he continued Etheridge and Carpenter's assignment of the species to *Metablastus*.

Recent developments in preparatory techniques have made it possible to expose hitherto obscured structures. A. Phillipot and M. Y. Milon kindly allowed the writer to further develop the specimen described by Phillipot with an air abrasive machine. By this means, it has been possible to determine that it has four spiracles and an anispiracle, thus separating it from *Metablastus*, which has paired spiracles. It appears to represent a valid genus, for which the name *Belocrinus* has priority. The writer studied the basal plate in the British Museum (Natural History) which was figured by Etheridge and Carpenter (E166). It is an isolated basal plate of the same type as is illustrated in Plate 39, fig. 7, and as are found in the complete specimen. These are all from Bois-Roux in France and belong to the same species. No type specimen was ever designated for this species; the complete specimen described and figured herein is designated the hypotype for nomenclatural purposes. It is described below and the ontogenetic development of the principal plates determined.

Acknowledgements. I would like to thank André Phillipot and M. Y. Milon (Institut de Géologie, Université de Rennes, Rennes) for allowing me to examine and prepare the specimen described in [Palaeontology, Vol. 9, Part 2, 1966, pp. 244-51, pl. 39.]

this paper; and R. P. S. Jefferies and Hugh Owen (British Museum (Natural History), London), for their help while studying the museum's blastoid collection. My studies in Europe were made possible by grants from the Museum of Paleontology, Horace H. Rackham School of Graduate Studies, and H. H. Power Education Trust for Faculty Travel, University of Michigan.

SYSTEMATIC DESCRIPTION

Class BLASTOIDEA

Order SPIRACULATA

Genus *BELOCRINUS* Munier-Chalmas 1881

Type species. *Belemuocrinus cottaldi* Munier-Chalmas.

1876 *Belemuocrinus* Munier-Chalmas, p. 105 (junior synonym of White 1862).

1881 *Belocrinus* Munier-Chalmas, p. 503.

1938 *Belocrinus* Munier-Chalmas; Bassler, p. 52.

1943 *Belocrinus* Munier-Chalmas; Bassler and Moodey, p. 212.

Generic diagnosis. Spiraculate blastoids with five spiracles, one of which is an anispiracle located between an epideltoid (?) and hypodeltoid (?), all deltoids quite visible in side view, a single pore occurring between adjacent side plates along radial and deltoid margins, lancet covered by side plates, calyx elongate club-shaped; large, massive basals; ten hydrosfire groups; number in each unknown.

Age. Lower Devonian, north-west France.

Remarks. The generic characters of this form are similar to those of the genus *Cordyloblastus* (see Fay 1964, p. 86) but present information indicates that they are separate genera. They each have five spiracles; the number of anal deltoids in *Belocrinus* is not clear, however, and they could be the same as in *Cordyloblastus*. The deltoids of these two forms apparently differ, there being an extensive external aboral growth sector in the former (see later). There also appear to be ambulacral pores along both the radials and deltoids of *Belocrinus*; Fay (1961, p. 54) described these as being absent along the deltoids in *Cordyloblastus* (see Pl. 39, figs. 9, 10). The basals of the former are also unusually pronounced, giving the calyx an extremely elongate appearance. In view of the uncertainty as to the configuration of the anal deltoids, however, it is recommended that the generic name *Belocrinus* should not be extended beyond *B. cottaldi* until the nature of the anal deltoids can be determined.

Belocrinus cottaldi (Munier-Chalmas)

Plate 39, figs. 1–8, 11

1876 *Belemuocrinus cottaldi* Munier-Chalmas, p. 105.

1877 *Belemuocrinus cottaldi* Munier-Chalmas; Delage, p. 81 (*non vide*).

1881 *Belocrinus cottaldi* (Munier-Chalmas); Munier-Chalmas, p. 503.

1882 *Belocrinus cottaldi*, (Munier-Chalmas); Oehlert, p. 362, pl. 9, figs. 3a–e.

1883 *Troostierinus cottaldi*? (Munier-Chalmas); Etheridge and Carpenter, p. 245.

1883 *Pentremiteidea cottaldi*? (Munier-Chalmas); Etheridge and Carpenter, p. 245.

1886 *Metablastus cottaldi* (Munier-Chalmas); Etheridge and Carpenter, pp. 201–3, pl. 5, fig. 22.

1899 *Metablastus cottaldi* (Munier-Chalmas); Bather, pp. 18, 19.

1938 *Belocrinus cottaldi* (Munier-Chalmas); Bassler, p. 52.

1943 *Belocrinus cottaldi* (Munier-Chalmas); Bassler and Moodey, p. 212.

1957 *Metablastus cottaldi* (Munier-Chalmas); Phillipot, pp. 64–68, text-figs. 1–5.

Description. Calyx elongate club-shaped in side view, pentagonal in oral view. Length 44.0 mm.; width 14.5 mm. Pelvis extremely long for a blastoid, massive, conical, flaring out gradually beneath ambulacra. Vault parabolic. Vault 13.7 mm., pelvis 30.3 mm.; pelvic angle 30°. Greatest width at ambulacral tips; cross-section pentagonal with slightly concave interambulacral areas.

Basalia three, azygous basal in AB interambulacral area (for terminology see Fay 1961), extremely massive, narrow, elongate. Azygous basal quadrate, slightly asymmetric; lower edges very narrow V shape, distal edges broader V; length 24.2 mm., width 5.7 mm. Point of origin located very near proximal tip. Growth has occurred on both distal and lateral edges. Plate has grown 20.3 mm. distally, 2.2 mm. laterally. When BR (distal) growth axis of azygous basal (see Pl. 39, fig. 8) reached 5.0 mm. from origin, interbasal (BB) 0.8 mm.; at 11.2 mm., BB 1.4 mm. If $BR + BB = 100\%$ total growth at a given increment, then BR at 5.0 = 86% total growth, at 11.2 = 88%, at 20.3 = 90%; thus BR accelerating relative to BB during ontogeny. Well-developed interbasal growth axis; sharp, elevated sides to azygous basal which become reduced distally. Upper surface very slightly convex. Fine growth-lines parallel to plate edges; 9 per mm. on BR axis.

Larger basals hexagonal; distal edges double V shape; lateral edges very narrow V shape. Sides sharply elevated due to interbasal growth axis. Upper surface very slightly convex. Length (to centre) 22.0 mm.; to one of points 24.3 mm.; width 9.3 mm.; distal (BR) growth axis 21.4 mm., growth front 5.1 mm. Fine growth-lines parallel sutures.

Three basalia together have a trigonal rounded cross section, slightly concave along sutures (Pl. 39, fig. 2). They taper abruptly proximally near base to form a small round facet for attachment of column (now chipped); attachment area 1.0 mm. in diameter; no crenellar facets preserved. Each large basal has a crack extending proximally from

EXPLANATION OF PLATE 39

Figs. 1, 2. Oral and basal views of only complete specimen of *Belocrinus cottaldi* Munier-Chalmas; anispiracle at 6 o'clock. Figs. 3–6, 8, and 11 of same specimen. $\times 2$.

Fig. 3. Inclined oral view of *B. cottaldi* at BC interambulacral area, showing reflected radiodeltoid suture and internal septum dividing spiracles. $\times 8$.

Fig. 4. Lateral A ambulacral view of *B. cottaldi*. $\times 2$.

Fig. 5. Enlarged oral view of *B. cottaldi* showing the four spiracles and the anispiracle (latter at 6 o'clock). Peristome in centre. $\times 8$.

Fig. 6. Aboral end of B ambulacrum, showing brachiolar facets, pore furrows, side and main food grooves, and cover plate lobes and furrows. $\times 8$.

Fig. 7. Isolated basal plate of *B. cottaldi*, UMMP 51144. $\times 2$.

Fig. 8. Enlarged view of basal plates of *B. cottaldi*, showing growth lines of interbasal (BB—vertical) and basal-radial (BR—inclined) sectors. Origins at lower corners of figure. $\times 4$.

Figs. 9, 10. Inclined B ambulacral and oral views of *Cordyloblastus eifelensis* (Roemer), USNM S5086, showing four spiracles and anispiracle (at 6 o'clock in fig. 10). Note presence of pores only along radials and presence of small deltoid body aboral to spiracles. $\times 8$.

Fig. 11. AB interambulacral view of *B. cottaldi*, showing growth-lines of radiodeltoid (RD—upper inclined), inter-radial (RR—vertical), and radial-basal (RB—lower inclined) sectors of radials. $\times 4$.



MACURDA, Devonian blastoid *Belocrinus*

the top centre. Each dies out before reaching origin of plate; growth-lines appear to cross without interruption. Apparently not a primary suture; significance unknown.

Radials five, narrow, elongate (aboral portion V shaped; lateral sides almost parallel), with deep narrow V for ambulacra (see Pl. 39, fig. 4). Height 3.1 mm.; width at base 5.3 mm., at ambulacral tip 6.5 mm., at deltoids 4.9 mm. Radial grew outwards in three directions from origin at aboral tip of ambulacrum (Pl. 39, fig. 11); 12.3 mm. towards radiodeltoid suture (RD axis), RD front (area along which calcite added) = 1.5 mm.; 5.3 mm. towards interrarial suture (RR axis), RR front 17.1 mm.; 8.9 mm. towards radial-basal suture (RB axis), RB front 5.0 mm. Earlier ontogenetic stages: when RR = 3.7 mm., RD = 8.2 mm. and RB = 5.1 mm. respectively; when RR = 2.0 mm., RD = 3.5 mm., RB = 2.7 mm. If $RD+RR+RB = 100\%$ of total growth at a given instance then following percentages found:

	RD	RR	RB
RR = 2.0 mm.	43%	24%	33%
= 3.7 mm.	48%	22%	30%
= 5.3 mm.	46%	20%	34%

Only RR shows a continuous trend, apparently slowing down; rate of growth of RD and RB appears to increase. Fine growth-lines parallel interrarial and radial-basal sutures; those parallel to radiodeltoid not as evident. Interrarial growth area ornamented by low, slightly irregular ridges parallel to interrarial suture (Pl. 39, fig. 11). Calcite of plates an endoskeleton, secreted by mesoderm. Layer of tissue between radial and basal plates secreted calcite on both edges simultaneously; rate of secretion by tissue between radials and basals 2.3 times faster on basal BR axis than on radial RB axis. Rate of growth of BR axis 3.8 times that of RR, 1.7 times that of RD.

Deltoids four, surround peristome (four regular plus anal deltoids). Length 3.8 mm. Adoral edge 0.7 mm. wide, forms border of peristome. Large single spiracle divides adoral portion from body (Pl. 39, fig. 5). Spiracle ovoid, diameter 1.1 mm. Septum arises 0.5 mm. below adoral edge of spiracle, divides it internally, and connects adoral and aboral portions of deltoid. Adoral edge of spiracle formed by adoral edge of deltoid, adoral lateral edges by adjacent lancet plates, aboral lateral edges by side plates, and aboral edge by adoral edge of aboral portion of deltoid. Latter part of plate is triangular, 3.0 mm. long; greatest aboral width at radiodeltoid suture 2.5 mm.; width just aboral to spiracle 0.5 mm. Radiodeltoid suture peculiar shape (Pl. 39, fig. 3). Portion adjacent to interrarial suture junction straight; half-way along radiodeltoid suture sharp bend adorally. Each leg 0.8 mm.; base of triangle 1.5 mm. Significance of shape unknown.

Ornamentation of deltoids obscure; apparently faint growth lines parallel to radiodeltoid suture.

Entire growth of deltoid 3.8 mm.; rate of growth of BR 5.3 times this, and RD 3.2, RR 1.4, RB 2.3 times respectively.

Anal spiracle an anispiracle, length 1.4 mm., width 1.3 mm. Number of anal deltoids uncertain, apparently an epi- and hypodeltoid (see below). Epideltoid forms part of edge of spiracle, width 1.0 mm. Internally, two prongs can be seen extending aborally to divide anal hydrosphere areas from anus but aboral ends obscured by matrix. Junction with aboral part of anal deltoids not visible. Portion of anal deltoids aboral to anispiracle presumably a hypodeltoid. Borders of anispiracle as for spiracles, except epideltoid

adoral edge, hypodeltoid aboral edge. Latter 0.9 mm. wide here (greater width than other deltoids to accommodate anus); greatest width at radiodeltoid suture 3.5 mm. Configuration of hyporadial suture as for regular radiodeltoid suture; inner leg of suture 1.2 mm., outer 0.5 mm.; length of base of triangle 1.6 mm. Length of hypodeltoid 3.7 mm. Full length of anal deltoids 4.7 mm. Ornamentation of hypodeltoid apparently as for regular deltoids.

Ambulacra five, linear, narrow, tapering gradually; slightly convex lengthwise. Length 13.7 mm., greatest width 2.2 mm. Lancet does not reach peristome except in one ambulacrum (weathering); normally begin 0.3 mm. from peristome. Lancet exposed only at most adoral end of ambulacrum. Two side plates per mm., 27 on one side of an ambulacrum. Side plates elongate, obliquely disposed to centre of ambulacrum (Pl. 39, fig. 6). Outer edge embayed by an elongate outer side plate which reaches outer edge of ambulacrum, and a pore which is formed by a notch on the adoral edge of the outer side plate and aboral edge of the side plate. Abmedial edge of pore formed by radial or deltoid. Cross-section of ambulacrum from main food groove to abmedial edge convex. Side plates slope upwards from food groove for one third of distance, then slope downwards remaining two-thirds. Abmedial edge about three times lower in cross-section than main food groove. Brachioles were attached to large, elongate, elliptical brachiolar facet, which was on the downward sloping outer edge of the side plates; axis of facet inclined adorally, upper edge being closer to oral area. Brachiolar facet located on side and outer side plates. Brachiolar food groove descended to ambulacrum at high point on cross-section of side plate, becoming a short side food groove which joins the main food groove. Latter ascended adorally. Cover plate lobes and furrows can be seen along main food groove; suggestion of presence along side food grooves as well. A long, narrow, adorally directed arcuate pore furrow originates near main food groove (but separate from it) admedially to crest of side plate, descends to the pore via a depression between adjacent high points where the brachiolar food groove meets the side food groove (Pl. 39, fig. 6). After passing through the depression it rests on the suture between the side plate and outer side plate. Judging from the brachiolar facet, brachioles were relatively large and elongate in cross-section but no trace now preserved.

Spiracles four plus an anispiracle; apparently ten hydrospire groups, but number in each unknown.

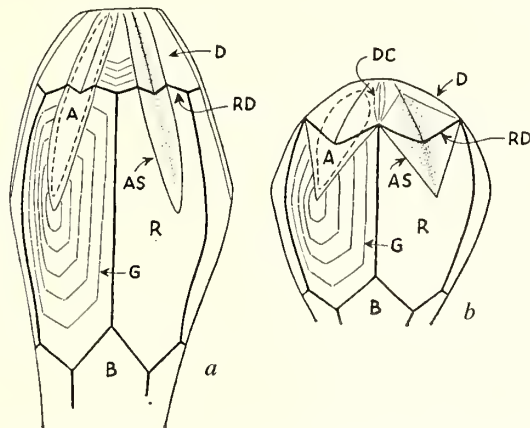
Peristome pentagonal; width 1.5 mm.

Remarks. The above description is based on the only known complete specimen which is in the collections of the Institut de Géologie, Université de Rennes, Rennes (Ille-et-Vilaine), France. The only other known material are basal plates.

The growth lines preserved on the plates of blastoids render them ideally suited for ontogenetic study. Ontogenetic data are presented above for the principal plates but the data are biased as there is no reflection of specific variation. However, ontogenetic studies in the Mississippian blastoid *Orophocrinus* (Macurda 1966) appear to indicate that ontogenetic curves derived from an individual or a series of individuals generally reflect the ontogenetic development of the species under study. The growth of the principal plates of blastoids proceeds by small increments which are added to the lateral edges of the plate. If there are simultaneous additions on all plates, the number of growth

lines along various growth axes should correspond with one another. This was analysed in this specimen but the results were inconclusive.

The size of the basal plates relative to the other plates is very unusual. Normally these are quite small, being confined to a relatively small area at the base of the calyx. It is also unusual for a measurable interbasal axis to be developed in blastoids.



TEXT-FIG. 1. Schematic diagrams of two blastoids showing differences in growth patterns in radials and deltoids in such genera as *Belocrinus* and *Orophocrinus* (fig. a) and *Phaenoblastus* and *Phaenoschisma* (fig. b). Ambulacral sinus (those parts of radials and deltoids which lie beneath ambulacra or slope steeply in toward them) indicated by AS. Ambulacra (A) proper have been removed; position indicated by dashed lines. Fig. a shows the configuration of growth-lines (G) in genera in which there is growth along the radiodeltoid suture external to the ambulacral sinus (RD). Note reflexed growth-lines by ambulacral sinus and presence on aboral portion of deltoid (D). Fig. b illustrates the case in which there is no growth external to the ambulacral sinus. Note lack of reflexed growth-lines by sinus and absence on aboral portion of deltoid, which is now a deltoid crest (DC). Basals indicated by B.

Belocrinus appears to be very similar to *Cordyloblastus*. In the latter genus, the deltoid is not exposed in side view (but there is a small edge of the deltoid body exposed aboral to the spiracle), while the deltoids of *Belocrinus cottaldi* are prominently developed in side view. The exposure or non-exposure of the deltoid is controlled by the developmental pattern of the plate; this is a reflection of the genetic make-up of the organism. In blastoid genera such as *Phaenoschisma* and *Phaenoblastus* (text-fig. 1), the aboral portion of the deltoid never grows outside the ambulacral sinus. Thus there are never any growth lines of the radiodeltoid front of the radial exposed outside the ambulacral sinus, growth occurring entirely within it. The growth-lines of the interrarial front extend up to the sinus and are never reflected as they are in genera such as *Orophocrinus* (text-fig. 1), where the deltoid grows external to the ambulacral sinus. The growth-lines in the radiodeltoid sectors of the radials in the AB interambulacral area of *Belocrinus cottaldi* (Pl. 39, fig. 11) appear to indicate that the deltoid has grown outside the ambulacral sinus throughout most, if not all, of its ontogeny, resulting in its exposure in side view. The growth-lines in the radiodeltoid sectors are not as evident as those of the

interradial, but can be seen perpendicular to the ambulacrum for most of the length of the radials which border the ambulacra. They are not evident near the aboral tip of the ambulacra as on the E side of the A radial; here the interradial growth-lines closely approach the ambulacra. The lack of radiodeltoid growth-lines in this sector may be a result of secondary secretions of calcite which have covered them, or of non-preservation.

The growth of the deltoid aboral to the spiracle appears to differ in *Belocrinus* and *Cordyloblastus*. The aboral body of the latter is little developed. However, the specimen of *B. cottaldi* described above is much larger than the average specimen of *Cordyloblastus*. It is possible that the deltoids of the species in the latter genus may develop a more prominent deltoid body later in their ontogeny.

The number of the anal deltoids in *Belocrinus* is unclear. A part of an anal deltoid plate borders the adoral side of the anispiracle. Two prongs can be seen arising from the aboral side of the plate. They are soon obscured by matrix and could not be developed further. They may possibly lead to cryptodeltoids or continue as prongs of an epideltoid. A large plate lies aboral to the anispiracle; its relation to the plate(s) described above is unclear. These are tentatively interpreted as an epideltoid and hypodeltoid respectively; further material is needed to determine the exact configuration of the anal deltoids. If there are two cryptodeltoids, it would indicate a close similarity to *Cordyloblastus*.

The ambulacral food grooves of *Belocrinus* were probably roofed over by cover plates which are known in genera such as *Pentremites* and *Orophocrinus*. The peristome is the highest topographic point on the calyx. There would have to have been some propulsive mechanism to force currents up the main food grooves to the peristome. This may have been accomplished by ciliary action. It should also be noted that the side food grooves are offset from one another and enter the main food groove at an angle of approximately 45 degrees (directed adorally) (Pl. 39, fig. 6). This inclination would seem to be the optimal hydraulic configuration. If they entered at a right angle, there would be a decrease in current velocity; additional energy would have to be expended to overcome this. If they are inclined, water from the side food grooves would merge with the currents in the main food groove with a minimum loss of energy. In addition, by having each one offset from the preceding one, increases in the volume of water are distributed over a greater area, rather than being concentrated at half as many points. Since the side food grooves are obliquely oriented, the brachiolar facets are as well. Thus the brachioles and brachiolar food grooves were obliquely oriented to the calyx. Whether this conferred any physiological advantage upon the blastoid is unclear at present.

Phillipot (1957, pp. 66, 67) recorded isolated basal cones in the collections at Rennes which reached a length of 35 to 40 mm. and noted that the complete specimens probably reached a length of about 70 mm., a large size for blastoids.

Plaster casts of the complete specimen have been deposited in the British Museum (Natural History), U.S. National Museum, and Museum of Paleontology, University of Michigan.

Occurrence. The specimen described above was collected by H. de Keravel from the limestones in the quarry at Bois-Roux, Gahard (Ille-et-Vilaine), to the north-east of Rennes, France (Phillipot 1957). Isolated basal cones have also been found at this

locality; it is now under water (Phillipot 1957, p. 64). Phillipot also recorded them from Joue'-en-Charnie and Brûlon in the department of the Sarthe (p. 64) and gave the horizon for all these localities as middle Siegenien (Lower Devonian) (p. 67). He stated that the Grès de Gahard horizon given by Etheridge and Carpenter (1886, pp. 200, 203) was incorrect.

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POPULATION STUDIES IN THE BALLYSHANNON LIMESTONE, BALLINA LIMESTONE, AND RINN POINT BEDS (VISÉAN) OF N.W. IRELAND

by J. A. E. B. HUBBARD

ABSTRACT. A numerical comparison of the populations of the outcrops formerly ascribed to the Ballyshannon Limestone and its lateral equivalents at Easky, Aughris, Serpent Rock, Streedagh, Kiln Port and Shalwy is presented. The localities define the limits of a subtrapezoidal area some 300 square miles in extent, in which the maximum distance between stations is 33 miles (Easky to Kiln Port) and the minimum 6.5 miles (Kiln Port to Shalwy). The four first named Sligo stations bear close similarities representing coral colonies, thickets, and even local coppices. The last two named Donegal stations have a different fauna which is not as dense and may be argued to represent either a different faunal province or, more probably, a different stratigraphical horizon. Aughris (Co. Donegal), near the type area of the Ballyshannon Limestone, is alluded to. It shows a distinctive fauna with affinities to the other Donegal stations though proportionally the assemblage is unique.

Stratigraphically the Donegal stations are regarded as belonging to the Ballyshannon Limestone (C_2S_1), while the Sligo stations are tentatively ascribed to the Benbulbin Shale—Glencar Limestone (S_2D_1) transitional phase.

Palaeoecologically all the faunas are regarded as having developed marginally between the dysphotic tropical belt and shallow warm waters of the open shelf. Of the Sligo stations Aughris is regarded as the most seaward facies of a coral biostrome. A niche biota faunal replacement of syringoporids by fasciculate lithostrotiontids, michelininiids by cerioid lithostrotiontids, narrow caniniids by giganteid forms, and daviseliids by linoproduc-tids is postulated.

THE Ballyshannon Limestone was first named and described by Oswald (1955, p. 168). He mentions that at Streedagh Point its thickly bedded argillaceous limestones and shales are extremely fossiliferous (p. 170). He continues by quoting Wynne (1864, p. 38) who describes the caniniids as '... like stumps in a cabbage garden, and one is almost disappointed to find that one can not pull them up; some of them are from 18 inches to 2 foot long and 2 to 3 inches in diameter'. Oswald adds that the description is apposite but corals are more numerous than it suggests. He mentions (p. 170) that similar beds are found at Serpent Rock; and cites another conspicuously fossiliferous outcrop between Fairies Bridge and Aughris (Co. Donegal).

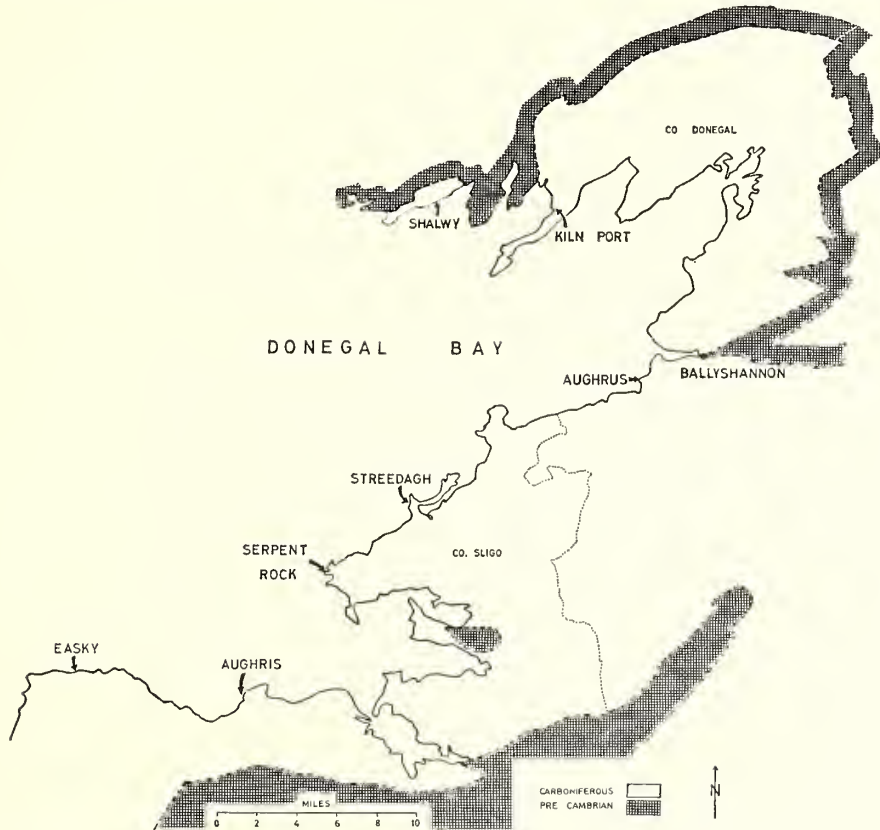
Bowes (unpublished Ph.D. thesis, 1957, p. 52) compares the Ballina Limestone with the Ballyshannon Limestone on lithological and faunal similarities, adding that their outcrops are virtually contiguous. He further describes the prolific faunas of the Ballina Limestone at Easky and Aughris.

George (*in* George and Oswald 1957, p. 143) places the Rinn Point Beds of Donegal high in the Ballyshannon Limestone, mentioning that they are better exposed in the Largymore syncline than on St. John's peninsula. Both outcrops are regarded as representatives of a mud-zone environment (p. 152). In the highest part of these beds, described in the eastern flank of the Largymore syncline, he draws attention to the very rich coral layers with large caniniids in a profusion comparable with that of Streedagh Point and Serpent Rock in the Lissadell Peninsula (Oswald 1955, p. 170).

To each of the above descriptions a fossil list giving generic and specific details is appended.

METHOD

Seven stations have been selected from extensive coastal exposures, chiefly in the intertidal zone, in which the partially silicified fauna is particularly well preserved. These localities are constituent of the previously designated Ballyshannon Limestone outcrop and its lateral equivalents. At each location, excluding Aughrus (Co. Donegal), 100 one-metre quadrants measured with a piece of string anchored by four pebbles were



TEXT-FIG. 1. Outline map of the Sligo-Donegal coast to show the location of the stations from which the population of the Ballyshannon Limestone has been sampled.

sampled. In each quadrant the total fauna, including entire and fragmental forms, above the size of comminuted crinoid debris, was counted. In order to obtain a representative sample bedding planes were studied at each locality.

At Aughrus (Co. Donegal), which is alluded to on account of its proximity to the type area of the Ballyshannon Limestone, it was found impracticable to sample more than 50 one-metre quadrants all of which are derived from the same bedding plane. Thus restricted, with only entire forms counted, no direct correlation may be drawn with this area though its significance is evident.

In the analysis of the fauna a specific identification has not been attempted. The

TABLE 1. Field counts on 100 one-metre quadrants

	EASKY		AUGHRIS		SERPENT ROCK		STREEDAGH		KILN PORT		SHAWY	
	a	b	a	b	a	b	a	b	a	b	a	b
SOLITARY CORALS												
caniniids	355	29	323	19	748	82	1050	82	91	8	329	49
zaphrentids	1		4		3		11		4		5	
clisiophyllids									6	7	28	
COMPOUND CORALS												
lithostrotiontids ₁	25	30	31	26	29	144	5	87				
lithostrotiontids ₂		740		550		861		375				
lithostrotiontids ₃	11		19	3	25	2	1					
syringoporids ₁									3		58	
syringoporids ₂									16		4	
syringoporids ₃											32	
auloporids	2	7	17	25	47	14	18	75	13		2	
micheliniids											30	1
BRACHIOPODS												
davisiellids			1						580		57	
chonetids									2			
linoproductoids	521	6			110	24	81	19				
pustulids				10				1	2	1		
productids	2	128				49					5	4
orthotetids	3				19	3	32	5	12			
leptaenids					10		4					
spiriferids		1			14		29	7	1			
rhynchonellids									2		1	
brachiopods+			6		28	117	69	174	39	70	3	2
BRYOZOA												
fenestellids	2	22		17		32		23		5	5	1
trepostomes	3	10		7		51		1				
TRILOBITES												
						5		2		1		
MOLLUSCS												
gastropods ₁			2		6		8					
gastropods ₂	3		3		23						25	
orthocones					1	1						
ECHINODERMS												
echinoids		1		1						27		
crinoid debris	GENERALLY		PRESENT		THROUGHOUT							
worm burrows	GENERALLY		PRESENT		THROUGHOUT							

The total population recorded in the field at Easky, Aughris, Serpent Rock, Streedagh, Kiln Port and Shalwy is tabulated.

Column (a) represents entire forms, column (b) fragmental forms.

Lithostrotiontids₁ fasciculate with corallites approximately 5 mm. in diameter.

Lithostrotiontids₂ fasciculate with corallites approximately 12 mm. in diameter.

This lithostrotiontid form was at first mistaken for fragmental material. The figures employed are the results of extrapolation. The majority of coralla were noticed to be composed of fewer than half a dozen corallites, often only two or four. To approximate the fragmental quota 10 per cent was

material involved, though prolific, is somewhat intractably set in a massive matrix which precludes detailed laboratory studies. Specimens are often only partially visible (Plate 41, fig. 2) and sometimes crushed by compaction. Thus brachiopod hinges are often buried or removed by erosion which would not allow for accuracy even at generic level though the profile available is adequate for the family or subfamily level of classification. Likewise it is argued that the selective sampling of corals would add no greater accuracy to this study when it is borne in mind that no less than 6,562 corals have been enumerated.

The faunal lists made available during the last decade by Bowes (1957, pp. 45–48), George and Oswald (1957, pp. 172–4), and Oswald (1955, p. 172) present the generic and specific details which are grouped in the present account. Of these Bowes' is the most localized, specifying Aughris as a collecting locality. Oswald (1955) unfortunately does not localize his material, of which much appears to have been collected from Streedagh Point and Serpent Rock, thus detracting from the significance of the Ballyshannon Limestone fauna quoted.

The Sligo outcrops, mentioned hereafter, consist of relatively thick, irregularly bedded, light grey biomicrite (Folk 1959) with a prolific coral-brachiopod fauna, and occasional thin shale partings. The fauna, which is scattered throughout, is particularly rich along certain planes. There is a tendency for one form to predominate in each stratum notably caniniids (Plate 40, fig. 1), lithostrotiontids (cerioid: Plates 40, figs. 2, 3, or fasciculate: Plate 41, fig. 1), or brachiopods; though a certain amount of mixing is to be found (Plate 41, fig. 2). The Donegal outcrops, by contrast, appear to be less fossiliferous, darker, more regularly bedded, somewhat impure biomicrites with a less silicified fauna.

The location of the stations (Easky, Aughris, Serpent Rock, Streedagh, Kiln Port, Shalwy, and Aughrus (Co. Donegal)) is indicated in text-fig. 1, with the total population as tabulated in the field in Table 1 and text-fig. 2. To simplify interpretation the genera were subsequently subdivided into five groups which seemed to have ecological significance: solitary corals, compound corals, brachiopods, bryozoa, and others which are plotted on histograms to show the varying proportions of entire to fragmental forms as a measure of turbulence.

Text-fig. 3 which represents the total numerical population shows a distinctly greater density of fragmental forms at Streedagh and Serpent Rock; these are closely followed by Easky in fragmental forms suggesting that these were the more turbulent areas. Kiln Port and Shalwy have a decidedly less dense fragmental population than the Sligo

discounted (a sum to which no statistical significance should be attached). The remaining 90 per cent. was divided by three to produce an approximate 'entire' quota. Thus in subsequent calculations the following numbers are used: Easky 222a 74b, Aughris 166a 55b, Serpent Rock 268a 86b, Streedagh 113a 37b.

Lithostrotiontids₃ cerioid forms.

Syringoporiids₁ with corallites approximately 2 mm. in diameter.

Syringoporiids₂ with corallites approximately 3 mm. in diameter.

Syringoporiids₃ with corallites approximately 4 mm. in diameter.

Brachiopods, unidentified short hinged.

Gastropods₁ fusiform.

Gastropods₂ helicoid.

stations and in 'entire' density are also comparatively sparse, indicating an indigenous fauna in less favourable though calm seas.

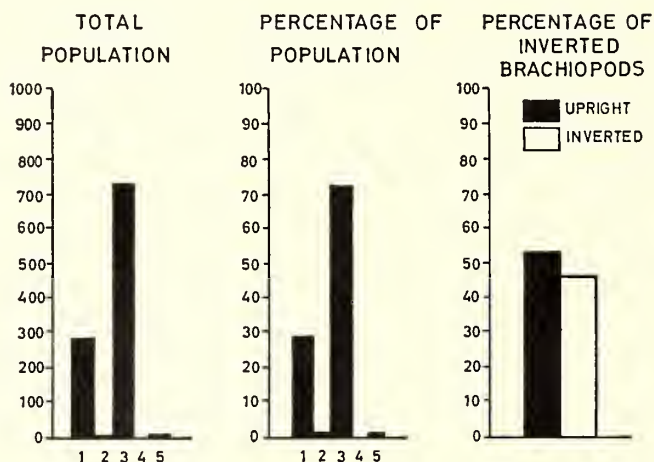
In text-fig. 4 the total population is expressed in a percentage histogram in which a similarity of distribution in forms is just discernible though less evident than in text-fig. 3. It is also to be noted that most specimens are entire, and of the fragmental fossils brachiopods and compound corals are generally dominant.

FIELD COUNTS

SOLITARY CORALS	
zaphrentids	287
COMPOUND CORALS	
auloporids	3
melchioriniids	2
BRACHIOPODS	
davisiellids	1
chonetids	2
pustulids	339
productids	69
rhynchonellids	319

worm burrows, crinoid,
echinoid and fenestellid
debris ubiquitous.

AUGHRUS (Co. Donegal)



TEXT-FIG. 2. The population of Aughrus (Co. Donegal). Field counts record the entire forms counted in 50 one-metre quadrats restricted to one bedding plane. Histogram of the total numerical population showing an anomalously high population which can be related to the selector bias of sampling only one bedding plane. Percentage histogram of total population resembling Kiln Port (text-fig. 5).

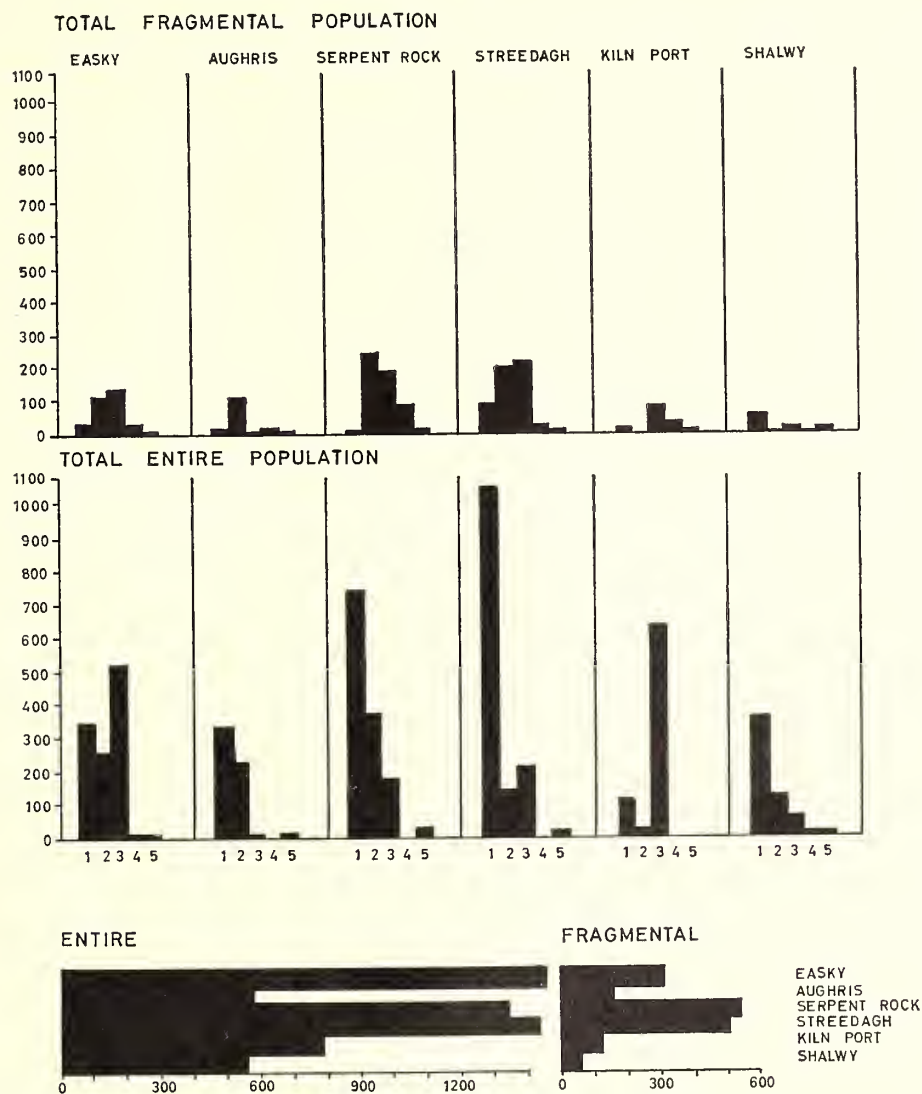
1, solitary corals. 2, compound corals. 3, brachiopods. 4, bryozoa. 5, others.

In text-fig. 5 a similarity in proportions of fragmental population is seen at Easky and Streedagh, while Shalwy and Serpent Rock show similar proportions for entire forms as also seen in text-fig. 4.

In text-fig. 6 the percentage of fragmental material within each group illustrates the abundance of fenestellid debris at Aughris, Serpent Rock, Streedagh, and Kiln Port. Aughris and Serpent Rock show a similar general population reflecting similar conditions of turbulence affecting the area despite initial differences in the faunal proportions seen in text-fig. 4. Shalwy, as in text-fig. 3, appears to have a comparatively small fragmental population in which the chief constituent is gastropods.

Inversion ratios shown in text-figs. 7 and 8 suggest mild turbulence in all areas, as more than 75 per cent. of brachiopods are inverted at all stations; while the corals are dominantly upright. Among the brachiopods no subfamily is present in all areas. In order to approximate similar hydrodynamic properties the larger forms of comparable profile were selected. Of necessity this resulted in the following forms being studied: linoproductids at the four Sligo stations, davisiellids at Kiln Port and Shalwy, and

pustulids at Aughrus (Co. Donegal). The state of preservation did not allow for the determination of whether or not the valves were joined, but since adductor muscles

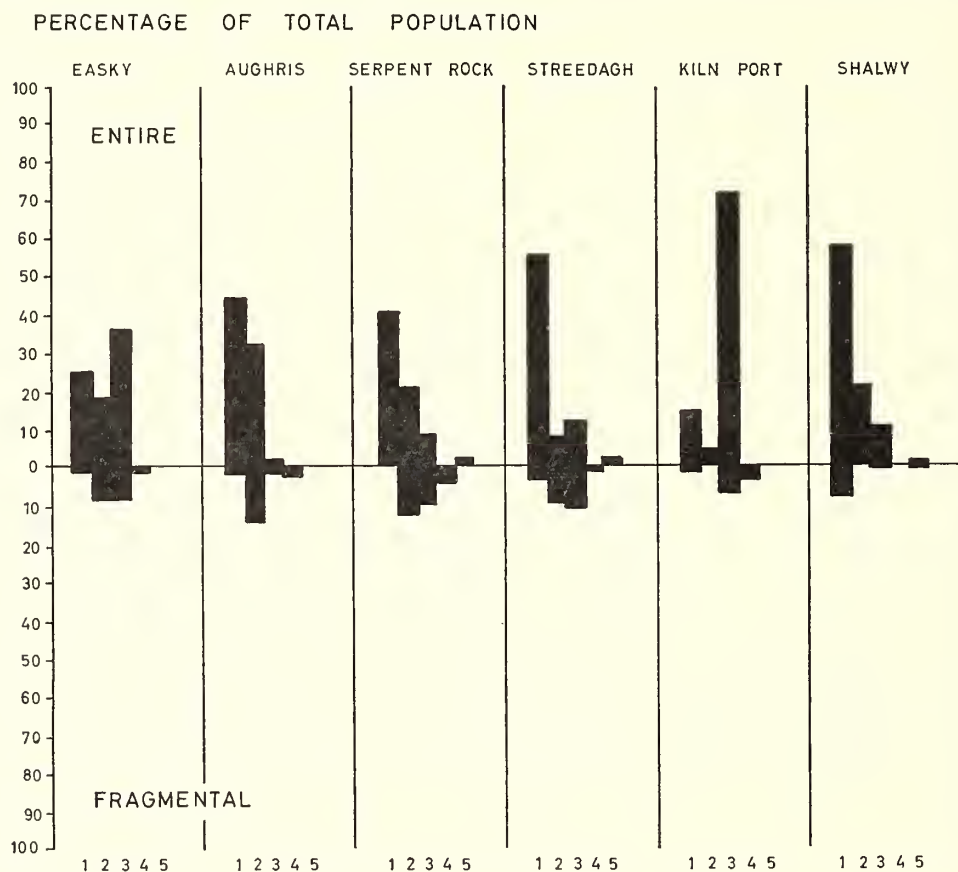


TEXT-FIG. 3. Histograms of the total numerical population, showing the dominance of entire over fragmental forms. On the fragmental population histogram Streedagh, Serpent Rock and Easky, in order of declining importance, show the greatest density. A similarity of proportions for the entire population is to be seen at Shalwy and Serpent Rock.

1, solitary corals. 2, compound corals. 3, brachiopods. 4, bryozoa. 5, others.

contract on death it is unlikely that this would be of great significance. In relation to the shell profile the brachiopods are described as upright when the pedicle valve is convex downwards on the bedding plane. Aughrus (Co. Donegal) would appear to be unique

in this study (text-fig. 7). The significance of the data would seem to be related to the number of sturdy spines for anchorage present. These are well developed only in the pustulids, while the linoproductids and davisellids are unattached forms more susceptible to current traction. Of the compound corals the cerioid lithostrotiontid with the



TEXT-FIG. 4. Percentage histogram for the total population showing the dominance of entire over fragmental forms. In comparison to the data expressed in fig. 2 the significance of given forms is accentuated.

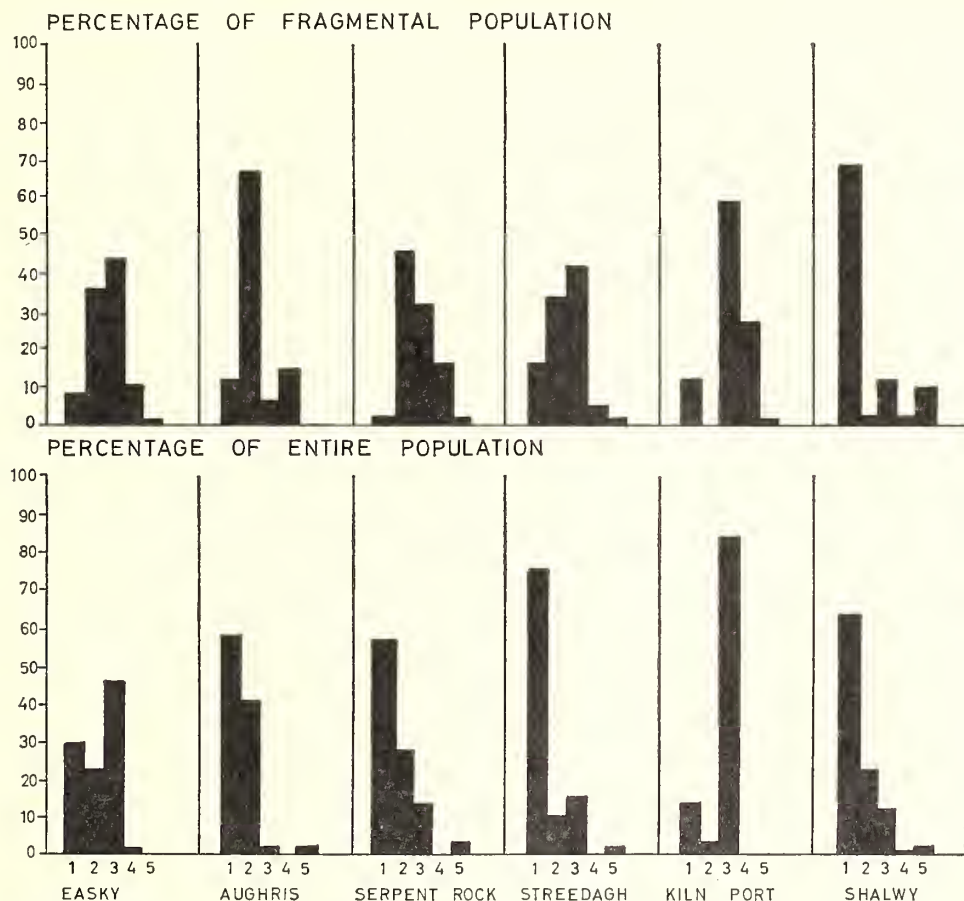
1, solitary corals. 2, compound corals. 3, brachiopods. 4, bryozoa. 5, others.

wider apical angle and generally more massive corallum is more stable than the fasciculate lithostrotiontid. Similarly the syringoporids of Shalwy are seen to be comparable with the fasciculate lithostrotiontids as a measure of stability.

The proportion of geniculate to straight caniniids shown in text-fig. 9 suggests that attachment of these forms to a soft lime substratum would not be sufficient to support the giganteid forms, which, while sinking, would tend to grow upwards towards the light. Three horizons are given for comparison at Streedagh (text-fig. 9) showing a uniformity which is not seen in the coral inversion ratios (text-fig. 8) for the same

area. The relationship between the straight and geniculate caniniids would appear to have no direct correlation with the size of the corallum or the species present.

The details of the Aughrus (Co. Donegal) (text-fig. 2) fauna show closest similarity with those of Kiln Port (text-fig. 3). Though the faunal list makes a striking contrast

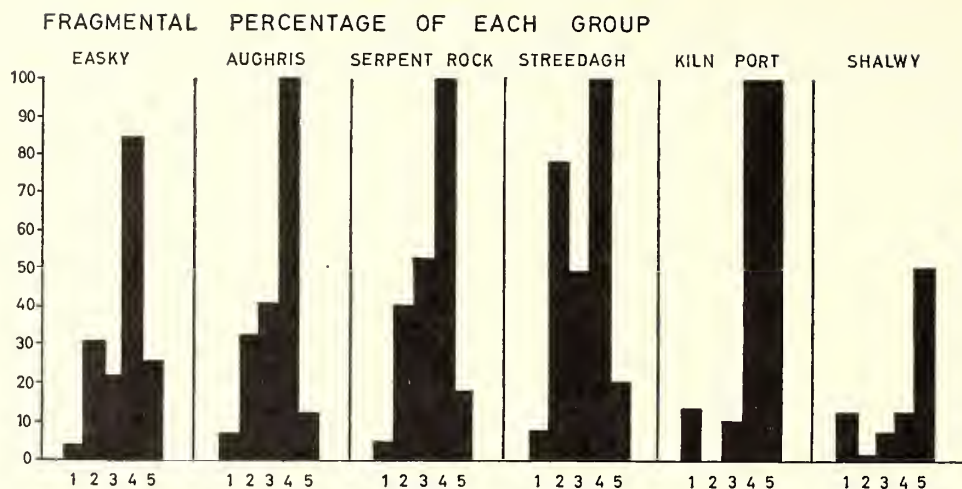


TEXT-FIG. 5. Percentage histograms of fragmental and entire populations. The reverse order of importance of fragmental material is to be seen at Serpent Rock and Streedagh, and of entire material at Streedagh and Kiln Port. Similar distribution for entire material is seen at Serpent Rock and Shalwy.

1, solitary corals. 2, compound corals. 3, brachiopods. 4, bryozoa. 5, others.

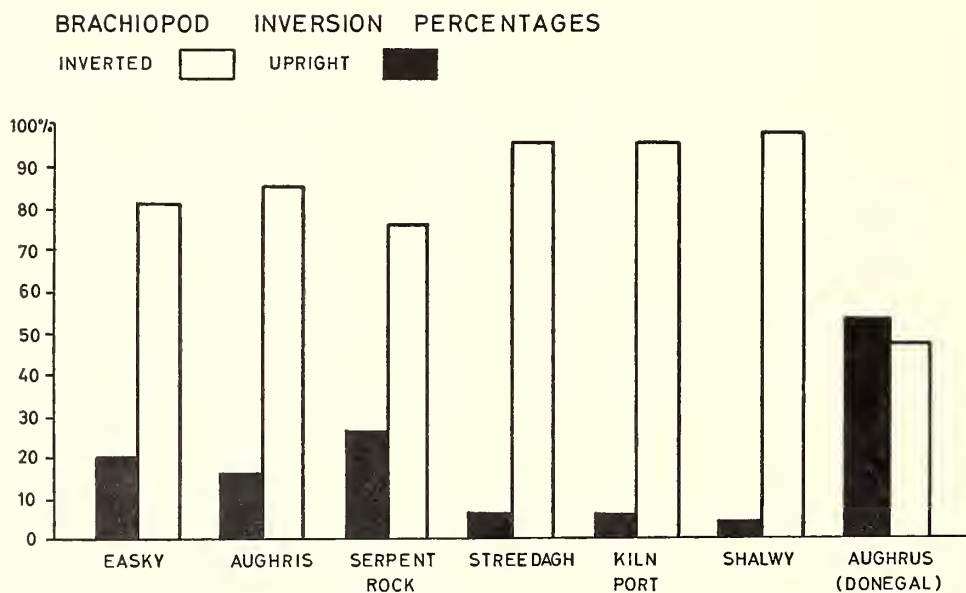
this can, in part, be attributed to the selector bias involved in sampling only one bedding plane. Caniniids and syringoporids, though not abundant, are to be found at this locality. Likewise euomphallids and *Conocardium*, which are not listed, also occur at the Donegal stations, though the latter is absent from the Sligo stations.

To attempt current analysis, orientations of crinoid stems from localities near the stations were recorded as well as umbonal orientations in inverted productoid



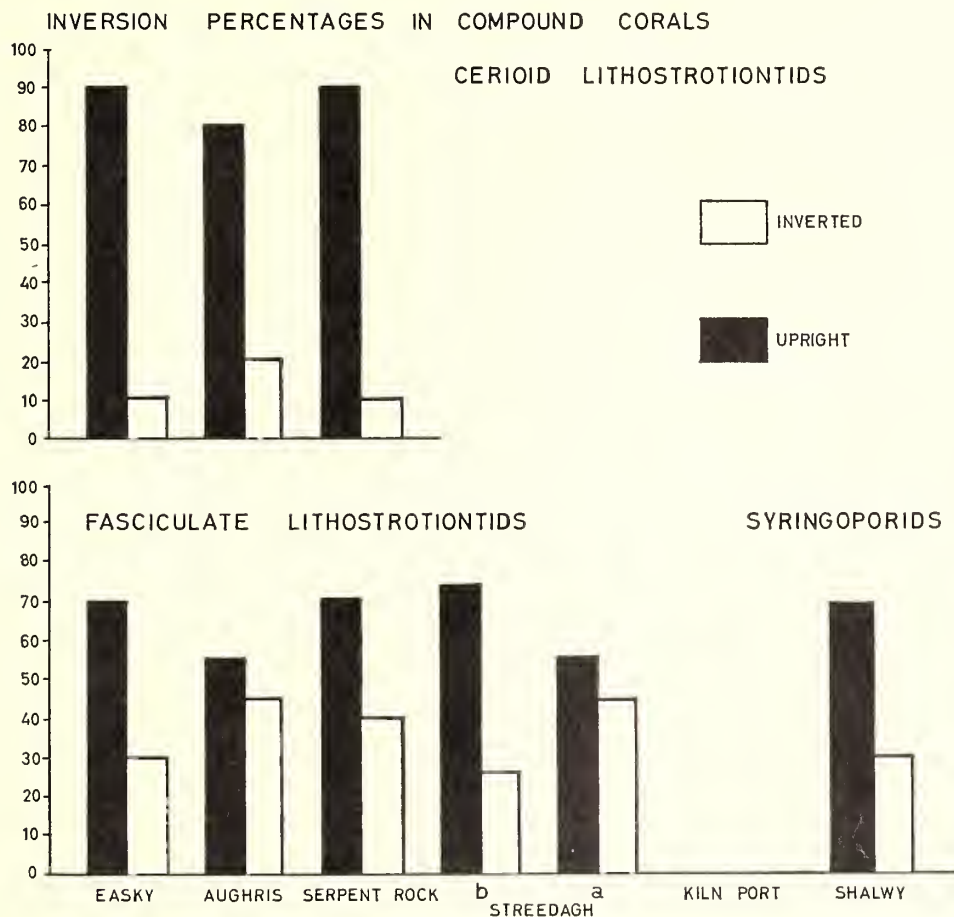
TEXT-FIG. 6. Percentage histogram of fragmental material expressed in terms of each group. A notable abundance of fragmental bryozoan material is to be seen at all stations except Shalwy. Aughris and Serpent Rock show similar population distributions.

1, solitary corals. 2, compound corals. 3, brachiopods. 4, bryozoa. 5, others.



TEXT-FIG. 7. Inversion ratios of productoid brachiopods (linoproductids at Easky, Aughris, Serpent Rock and Streedagh; davisellids at Kiln Port and Shalwy; pustulids at Aughrus (Co. Donegal)) expressed in terms of percentage histograms. A dominance of inverted forms is to be noted at all stations except Aughrus (Co. Donegal).

brachiopods, and the orientation of geniculate caniniids. The results are variable and inconclusive but never suggest transport from the south, thus generally supporting the palaeogeographical reconstruction presented by George (1958). This pattern is one which might be expected in an area with such a uniform population density and lack of evidence of channeling.



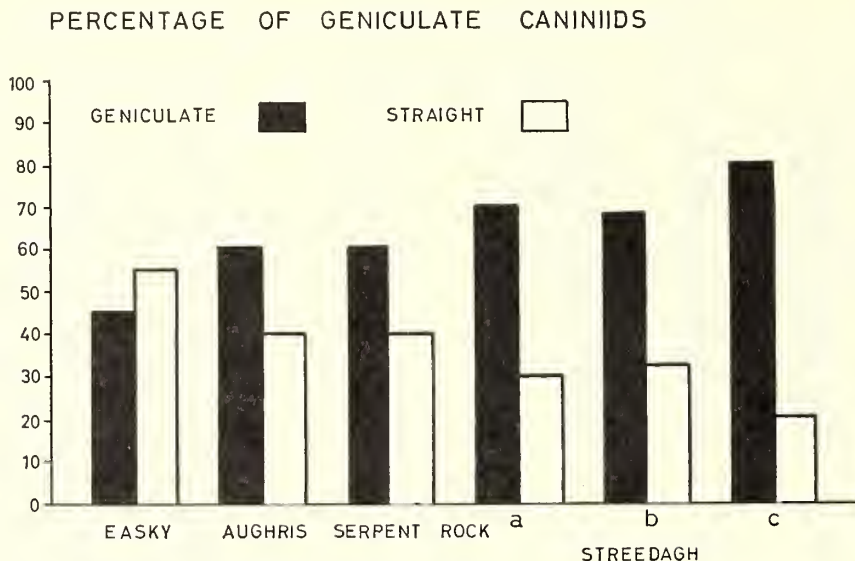
TEXT-FIG. 8. Inversion ratios of compound corals expressed as percentage histograms. Cerioid lithostrotiontids shown for Easky, Aughris, and Serpent Rock are dominantly upright. Fasciculate lithostrotiontids at Easky, Aughris, Serpent Rock and two horizons at Streedagh, and syringoporids of Shalwy show a less pronounced dominance of upright forms.

ENVIRONMENT

The fauna outlined above may be described in terms of Hill's (1948, p. 121) three coral associations. She showed these to have different morphological characters which varied according to the environment. Thus by analogy with present day faunas she reaches the conclusions tabulated (Table 2).

In text-fig. 10 the populations of this account are plotted on a triangular diagram

whose apices represent Hill's coral associations. This diagram supports her statement that solitary *Rugosa* with dissepiments are found associated with the compound *Rugosa*, but rarely with the *Cyathaxonia* fauna. In generalized terms the total fauna may be ascribed to her intermediate fauna of solitary *Rugosa*. However, when the beds are studied more closely, it would appear that there are alternations of the compound and



TEXT-FIG. 9. Ratio of straight to geniculate caniniids expressed in terms of a percentage histogram for Easky, Aughris, Serpent Rock, and three horizons at Streedagh. At all stations except Easky geniculate forms are dominant, notably at Streedagh.

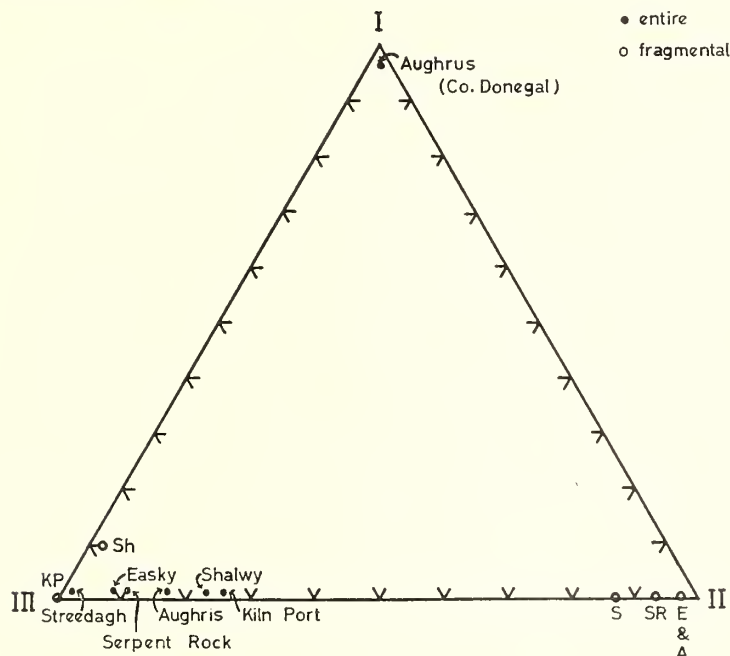
solitary *Rugosa* faunas within a few feet as illustrated in text-fig. 11, and Plates 40 and 41.

TABLE 2. Hill's (1948) three coral associations tabulated to show the relationship between the faunal characteristics and the modern analogy and environment.

FAUNAL CHARACTERISTICS	MODERN ANALOGY AND ENVIRONMENT
I <i>Cyathaxonia</i> Fauna small, solitary, non-dissepimented forms.	small, solitary, corals cold, deep or murky sea.
II Compound <i>Rugosa</i> & <i>Chaetetida</i> .	reef corals. warm, shallow, pellucid sea
III Solitary <i>Rugosa</i> with dissepiments (chiefly caniniids & clisiophyllids)	intermediate between I & II.

The palaeoecological conclusions quoted by Wells (in 1957, p. 774) have, until recently, been accepted widely for the limitation of rugosan habitats. Thus by analogy to present day, non-surface, essentially lagoonal reef corals he states that the ecological

niche has the following parameters: (1) a maximum depth of about 50 metres; (2) well within the pellucid zone; (3) annual minimum temperature of 16–21° C; (4) well oxygenated, gently circulating waters; (5) on a substratum clear or relatively free from rapid sedimentation, but not necessarily in clear non-turbid waters.



TEXT-FIG. 10. The coral populations of Easky, Aughris, Serpent Rock, Streedagh, Kiln Port, Shalwy, and Aughrus (Co. Donegal) are expressed in terms of Hill's three coral associations showing that the entire forms belong to the solitary *Rugosa* association.

- I. *Cyathaxonia* fauna: small, solitary, non-dissepimented forms.
- II. Compound *Rugosa* and *Chaetetida*.
- III. Solitary *Rugosa* with dissepiments (chiefly caniniids and clisiophyllids).

Teichert (1958, p. 1064), however, reminds us of Dons's (1933) and Shott's (1926) works in giving an account of cold deep water coral banks which are alive today off the coast of Norway. Thus he divides the modern scleractinian corals into two major ecological groups: the first of these, the Hermatypic, are dependent on the symbiotic flagellates, the zooxanthellae, and consequently restricted to an annual minimum water temperature of 18.5° C, and 300 ft. depth. Teichert's second group of Ahermatypic scleractinian corals are not dependent on zooxanthellae, and therefore are not restricted to the pellucid zones. These Hermatypic conditions would appear to be similar to those outlined by Wells (op. cit.). The degree of tolerance of the Ahermatypic group is wide, members having been recorded at depths of up to 20,000 feet, and temperatures as low as -1.1° C, though the majority occur at depths of 600–900 ft.

Teichert (1958, p. 1075) concludes that the best measure of depth is the presence of calcareous algae which are not found below 150 ft. From comparison with the

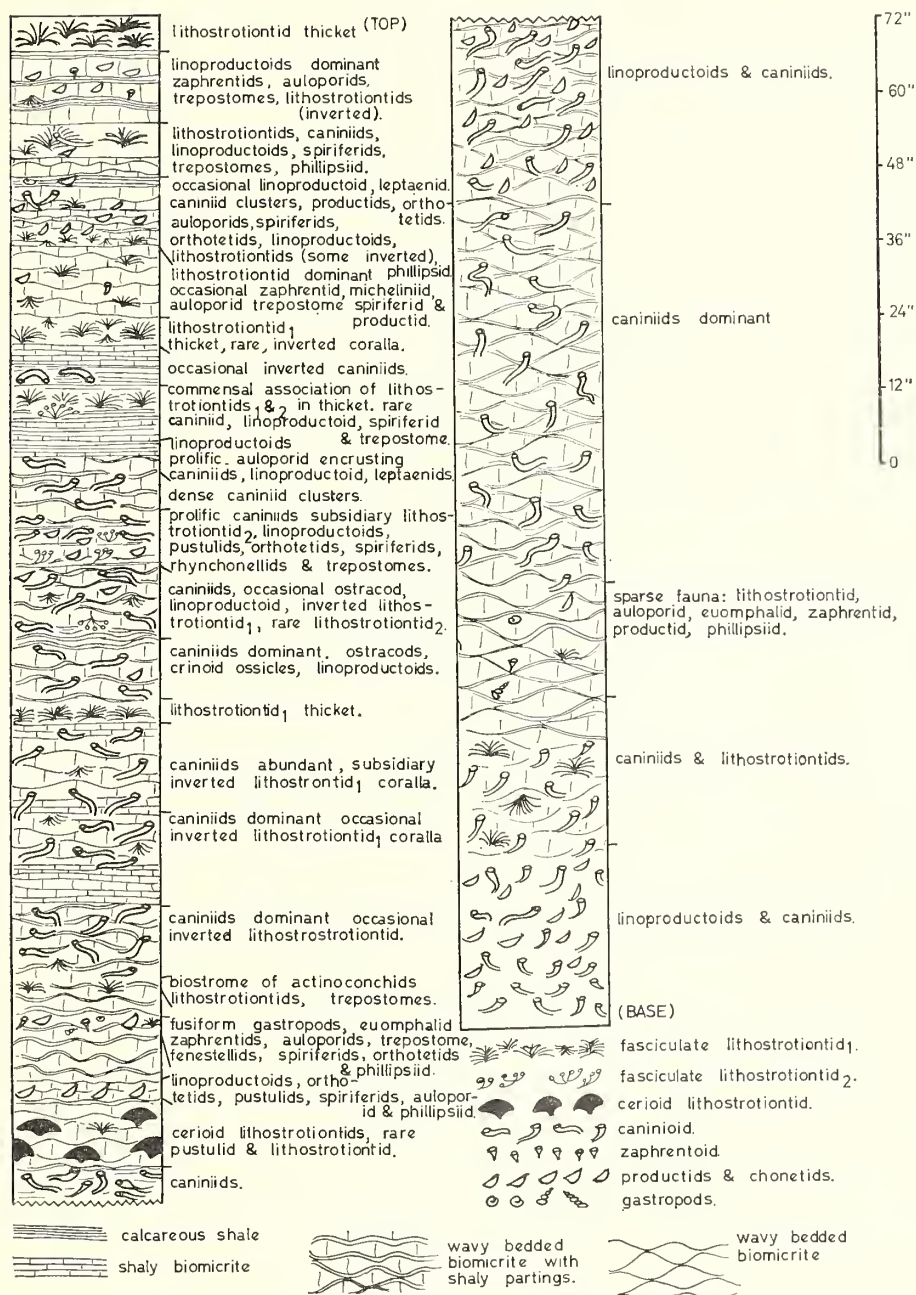
environments and biota tabulated (p. 1076) it would appear that the fauna described herein probably belongs to Teichert's category number 1. In this few species of frame building coelenterates with rich invertebrate association and absence of calcareous algae are recorded. This category is found in deep and cool waters, shelf or bay environments, within the temperature range of the dysphotic zone of the tropical belt to the polar regions. This contrasts with his category number 4, in which a rich assemblage of frame building coelenterates, in association with a rich invertebrate fauna, with the addition of abundant calcareous algae, is attributed to shallow warm waters in open shelf to near shore environments of the tropical belt. Calcareous algae are not obvious in the Irish coral limestone populations described here, though their presence has been noted elsewhere in the succession both above and below this horizon. This would suggest that the environment was probably marginal to the tropical dysphotic belt.

The development of conspicuously fossiliferous bedding planes alternating with less fossiliferous bands has been attributed by Broadhurst (1964, pp. 866 and 867) to the rate of sedimentation and the associated amount of bottom turbulence in the non-marine Coal Measures. On this view each fossiliferous plane represents a phase of restricted sedimentation. Teichert (1958, p. 1073) states that bioherms may show signs of sudden extinction, in which the destruction of the coral frame results from the attack of boring organisms, yet evidence of wave destruction is absent. He continues by saying that though this might be regarded as evidence of subsidence and consequent 'drowning' of the reef, it might equally well result from the elevation of the sea floor above the level of tolerance of the corals. In these beds there is evidence of extensive burrowing in both horizontal and vertical directions. From the infill of the burrows it is apparent that there was a variation in the nature of the sediment supplied. There is also abundant evidence of auloporids encrusting brachiopods, caniniids, and even occasional syringoporids, not infrequently in the position of growth, at Shalwy, Kiln Port, and Easky. This might be interpreted as a sign of a decline in sedimentational rate.

The fasciculate lithostrotiontid associations may chiefly be described as thickets, though occasionally there is evidence of coppice (Plate 41, fig. 1) development (Squires 1964, pp. 904-6). An unusual relationship is seen in one place at Serpent Rock where caniniids have been observed penetrating a fasciculate lithostrotiontid colony (Plate 41, fig. 3); this appears to be a commensal association. A similar relationship between two lithostrotiontids is seen high in the succession at Streedagh (text-fig. 11).

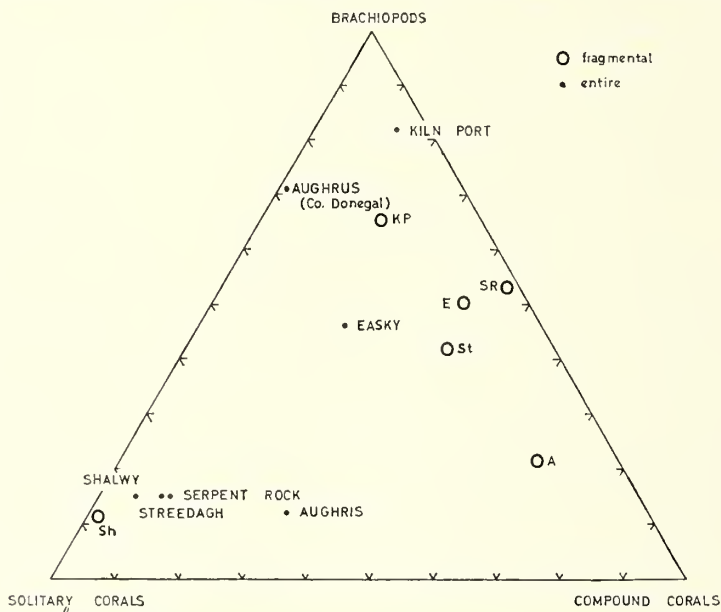
The cerioid lithostrotiontids, by contrast, seem to have an unsociable habit, commonly occurring on separate bedding planes from the other faunas where there is a distinct paucity of other fossils save trace fossils. The individuals thus appear as well separated colonies (Plate 40, figs. 2 and 3) in bioturbated biomicrites. An exception to this rule is seen near Easky pier where the coral brachiopod fauna is notably mixed, containing lithostrotiontids (fasciculate and cerioid), pustulids, chonetids, productids, and even rare caniniids which would suggest that the fauna may in part be transported.

The population is summarized in terms of the dominant ecologically significant groups in text-fig. 12. In entire population close similarities are seen at Shalwy, Streedagh, Serpent Rock characterized by a dominance of solitary corals, and few compound corals and brachiopods, indicating calm well aerated shallow seas. Aughris and Easky have fewer solitary corals but have more compound corals and brachiopods respectively, suggesting that more stable forms were tolerant of a somewhat greater turbulence. Kiln



TEXT-FIG. 11. Diagrammatic representation of the lithology of the coral limestone horizon within the Ballyshannon Limestone of Streedagh to illustrate the rapid alternation of Hill's coral associations.

Port and Aughrus (Co. Donegal) are anomalous in showing a marked preponderance of brachiopods over all other forms. The fragmental populations at Easky, Streedagh and Serpent Rock have marked similarity with a decrease in the number of solitary



TEXT-FIG. 12. The population of the Ballyshannon Limestone summarized in terms of the three dominant ecologically significant groups: brachiopods, compound corals and solitary corals. A close similarity is seen between the entire forms of Shalwy, Aughris, Streedagh, and Serpent Rock, while a secondary, less conspicuous group is formed by Easky, Kiln Port, and Aughrus (Co. Donegal). Of the fragmental population Streedagh, Easky, and Serpent Rock are particularly similar, with Kiln Port and Aughris showing a certain amount of similarity while Shalwy remains anomalous.

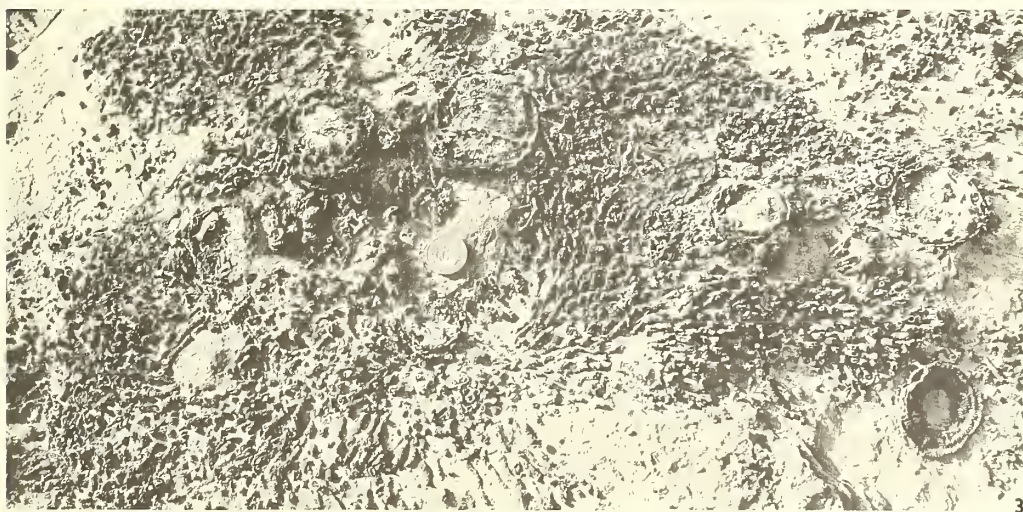
EXPLANATION OF PLATE 40

- Fig. 1. Portion of a bedding plane at Streedagh showing prolific partially silicified caniniids with variable degree of geniculation, set in a biomicrite matrix. Scale: hammer measures 13 inches.
 Fig. 2. Bedding plane at Serpent Rock showing well spaced cerioid lithostrotiontid colonies appearing as lighter coloured patches in the jointed biomicrite matrix. Scale: hammer 13 inches long.
 Fig. 3. Close-up of a cerioid lithostrotiontid colony *in situ* with horizontal burrow to the left of it, from the same bedding plane as fig. 2 at Serpent Rock. Scale: coin measures one inch in diameter.

EXPLANATION OF PLATE 41

- Fig. 1. Fasciculate lithostrotiontid coppice showing fragmental lithostrotiontid corallites in the lower portion of the stratum from which one large upright fasciculate lithostrotiontid corallum protrudes. Scale: hammer measures 13 inches.
 Fig. 2. Mixed caniniid, fasciculate lithostrotiontids 1 & 2 and brachiopod fauna, worn smooth by wave action; illustrating the impracticability of detailed identification of many intractable forms. Scale: half the magnification of fig. 1.
 Fig. 3. Apparently commensal association of caniniids and lithostrotiontid thicket at Serpent Rock. Scale: coin measures one inch in diameter.





corals present, possibly indicating that the solitary corals are more resistant on account of their thicker skeletons. Aughris likewise shows a proportional decrease in solitary corals. Kiln Port is once more anomalous in showing an increase in the number of both compound and solitary corals present. This may represent a fauna which has been transported further from the source of coralline material. It may be suggested that Streedagh, Serpent Rock, and Shalwy represent solitary coral biostromes in quiet seas while Aughris was on the rougher seaward side sustaining a greater proportion of hydrodynamically more stable forms. Kiln Port may represent more muddy seas with a vagrant benthonic fauna of brachiopods which developed on the landward side of the coral biostrome where a more restricted circulation would not favour coral growth.

Easky, Serpent Rock, and Streedagh may thus be regarded as an inshore, and Aughris a further seaward facies of a coral biostrome. These conclusions support the palaeogeography postulated by George (1958).

CONCLUSIONS

Variations in environment are clearly not the sole factor since there are faunal differences between the Donegal stations and those of Sligo. Thus in general the Donegal fauna consists of syringoporids, micheliniids, a relatively narrow caniniid and davisielids which are replaced by fasciculate and cerioid lithostrotiontids, giganteid caniniids and linoproductids in Sligo. It is not yet known whether these represent niche biotas of different faunal provinces or whether they are at different horizons, though the latter is suspected. In Sligo the former association can be traced low in the succession. Additional support for the latter argument has been reached independently on gross lithological grounds by W. F. Hubbard and D. J. R. Sheridan (personal communication) and on detailed foraminiferal studies by R. W. L. Oldroyd (personal communication). However, until further detailed macropalaeontological and micropalaeontological dating elucidates this problem, it could be argued that this faunal replacement results from the diachronous northward migration of faunas.

It would appear highly probable that the Sligo outcrops are of approximately the same age but of a different age to the Donegal outcrops. In support of this hypothesis the dating of the underlying Carrowmorán Sandstone found in the ground between Easky and Aughris is crucial. The Carrowmorán Sandstone has been shown by the author (1966, in press) to correlate with the Mullaghmore Sandstone of Sligo, to which an age between S_2 - D_1 has been ascribed by Oswald (1955, pp. 173, 174, and 180) on the basis of lithological comparison and ostracod dating. Furthermore the Ballyshannon Limestone of the coastal regions of Sligo from which these population studies are derived is shown to contrast strongly with that of the type area, yet it resembles higher stratigraphical horizons only six miles away. In the type area about Ballyshannon the Ballyshannon Limestone consists of massive crinoidal biomicrites, biosparites, and oomicrites containing mainly fragmental or transported fossils among which cerioid lithostrotiontids are not recorded. The lowest record of cerioid lithostrotiontids outside Oswald's (1955) area is in S_2 beds of Garwood (1913, p. 547). The second lithological comparison concerns Oswald's (1955) transitional Benbulbin Shale-Glencar Limestone (S_2D_1) exposed on the south-western flanks of Benbulbin Mountain, where four recognizable units, one of which is the coral-brachiopod limestone mentioned, can be

correlated with similar units at Streedagh and Serpent Rock. Similarly material of comparable lithology to the type section of the Ballyshannon Limestone has been recorded on bore-hole cores which penetrate the basement to the south of the outcrops herein described. Thus it would appear that the Sligo outcrops under discussion are referable to Oswald's (1955) Benbulbin Shale–Glencar Limestone (S_2D_1).

Reference to the faunal lists of Bowes (1957), George and Oswald (1957) and Oswald (1955) shows that the following corals are not present in the south-eastern flank of the Donegal syncline but are to be found in Sligo. At Aughris: *Caninia benburbensis* Lewis and *Lithostrotion pauciradiale* (McCoy). In Oswald's (1955) Ballyshannon Limestone list derived from the total outcrop: *Zaphrentis (Hapsiphyllum) konincki* (Edwards and Haime), *Lithostrotion affine* Fleming, *Lithostrotion martini* Edwards and Haime, and *Lithostrotion portlocki* (Bronn). To the south of this area Caldwell (1959, pp. 168, 180) does not record these species below the Ballymore Beds which he correlates with the Benbulbin Shale.

In contrast to the situation in Sligo the Donegal outcrops are known to be relatively close to the base of the Carboniferous succession and do not contain cerioid lithostrotiontids, even fasciculate lithostrotiontids being extremely scarce.

Environmentally it would appear that the Sligo fauna represents a similar ecological niche to that of Donegal; having developed marginally between the dysphotic tropical belt and shallow warm waters of the open shelf. The Sligo fauna is not present in the Donegal assemblage, yet occasionally Donegal members are still present in the Sligo fauna indicating that the dominant incoming fauna had not entirely excluded the earlier forms. It is suggested that there is a general replacement of syringoporids by fasciculate lithostrotiontids, narrow by giganteid caniniids, and daviselliids by linoproductids. Each of these pairs, being analogous forms, would appear to occupy the same ecological niche. The greater density and diversity of the Sligo fauna would suggest the attainment of more favourable conditions during the later Viséan, by which time the Carboniferous marine transgression had become established.

Acknowledgements. The author is indebted to Dr. G. M. Dunlop and Professor T. Neville George for the interest and encouragement shown during the course of the work; to Mr. J. W. Keith for technical assistance; and to Dr. C. H. Holland and Professor B. C. King for critically reading the manuscript, and the latter for supervision of the work which was carried out under the tenure of a D.S.I.R. Studentship at Bedford College (University of London).

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OCCURRENCE OF *AUSTRALOSUTURA* (TRILOBITA) IN THE MISSISSIPPIAN OF OKLAHOMA, U.S.A.

by ALLEN R. ORMISTON

ABSTRACT. A species of *Australosutura* is described from Mississippian rocks of Oklahoma regarded as being Viséan in age. It is most like the earlier-described Australian species, less like that from Argentina.

A TRILOBITE collected by Dr. Kenneth W. Ciriacks in the course of his investigation of the Moorefield Formation of Oklahoma was identified by me as *Australosutura*. In the company of Dr. Ciriacks I visited the locality from which the original specimen came and was able to collect additional material. These Oklahoma specimens are the first of the genus in North America.

So far as the writer is aware, *Australosutura* has previously been known to occur only in Australia and Argentina. Amos, Campbell, and Goldring (1960, p. 229) erected the genus for the single species *Cordania gardneri* Mitchell 1922, originally described from the Carboniferous of Australia. *A. gardneri* was recognized by them in collections from Argentina as well as from Australia. Another Australian occurrence of the genus was reported by Campbell and Engel (1963, p. 110).

Acknowledgements. I am indebted to Pan American Petroleum Corporation for permission to publish this paper. I thank Dr. K. W. Ciriacks of the Research Center of Pan American Petroleum Corporation for making available to me the first Oklahoma specimen of *Australosutura* and for his help in collecting more material. Dr. Gilbert Klapper, also of the Research Center, kindly provided age information based on his studies of selected conodont faunas from the Moorefield Formation. My wife, Eleanor, collected the only pygidium of *Australosutura* we have been able to find.

Stratigraphy. The north-eastern Oklahoma exposures of the Mississippian Moorefield Formation were divided by Huffman (1958, p. 49) into four members which are in ascending order: the Tahlequah, Bayou Manard, Lindsey Bridge, and Ordinance Plant Members. All the specimens of *Australosutura* described in this paper come from a 6-in. bed 8·7 to 9·2 ft. below the top of the Bayou Manard Member exposed in the bed of a dry stream 0·5 miles south of Welling, Oklahoma (exact locality information below). At this locality the Moorefield Formation is incompletely exposed; the lowest beds being within the Bayou Manard Member. Approximately 30 miles north-west of the Welling locality there is a complete exposure of the Moorefield Formation at Lindsey Bridge. There the entire formation is 107 ft. thick and the Bayou Manard Member 53 ft. thick. Although the Welling exposure is incomplete, the Bayou Manard Member appears to be considerably thinner there than at Lindsey Bridge.

At Welling the Bayou Manard Member consists of dark gray to black, argillaceous, micritic limestones, and calcareous shales.

Bayou Manard Fauna. The bed from which *Australosutura* was collected yields a fairly diverse fauna including brachiopods, pelecypods, and trilobites. By far the most

abundant elements are *Cleiothyridina* sp. and the trilobite, *Griffithides pustulosus* Snider 1915. Less common are: *Spirifer arkansanum* Girty 1911; *Neochonetes* sp.; two genera of productids; and ?*Sphenotus* sp.

Age. According to Dr. Gilbert Klapper (personal communication) the conodont fauna present in the *Australosutura*-bearing bed of the Bayou Manard Member belongs to the *Gnathodus bilineatus*-*Cavusgnathus characta* Zone of Collinson *et al.* (1962). This bed of the Bayou Manard Member is thus Viséan in terms of the European chronology (see Collinson *et al.* 1962, p. 13, chart 5).

The Argentinian occurrence of *A. gardneri* (Mitchell) has also been suggested to be Viséan in age, whereas the Australian occurrences are considered Westphalian (Amos, Campbell, and Goldring 1960, p. 229). The disparity in age between the Argentine and Australian material of *A. gardneri* led Campbell and Engel (1963, p. 112) to suggest that those occurrences represent separate species. Elsewhere in this paper are noted morphologic differences which support this suggestion, but considering the Viséan Oklahoma *Australosutura* to be closely related to the Westphalian *A. gardneri* from Australia implies that the species really is long ranging.

SYSTEMATIC DESCRIPTION

Family BRACHYMETOPIDAE Prantl and Přibyl 1951

Genus AUSTRALOSUTURA Campbell and Goldring 1960

Type species. *Cordania gardneri* Mitchell 1922.

Australosutura aff. *A. gardneri* (Mitchell 1922)

Plate 42, figs. 1-9

Material. USNM No. 145307, an incomplete cephalon lacking the left free cheek; USNM No. 145308, a small partly exfoliated cranium; USNM No. 145309, a fragmentary cephalon preserving the left genal spine; and USNM No. 145310, a pygidium preserved as an internal mold.

Locality and Horizon. A bed 8·7 to 9·2 feet below the top of the Bayou Manard Member, Moorefield Formation, bank of a dry stream which runs generally north-south through the pasture of Mrs. S. Brackett's farm, SE 1/4, SE 1/4, section 7, T. 16 N., R. 23 E., Cherokee County, Oklahoma.

Description. There are no consistent differences in the cephalon between the Oklahoma and Australian specimens (Amos, Campbell, and Goldring 1960, p. 234, pl. 40) of *Australosutura* with the possible exception of one minor character. The tubercles present along the posterior slope of the anterior and lateral cephalic borders appear to be more prominent on the Oklahoma specimens.

The Argentinian specimens assigned to *A. gardneri* by Amos, Campbell, and Goldring (1960, p. 230) do, however, differ importantly from the Oklahoma material. They are distinguished in having: (1) the cephalon more strongly inflated, (2) the anterior part of glabella rising vertically in lateral profile, (3) the frontal area distinctly shorter (sag.), and (4) the glabellar tuberculation finer than that elsewhere on the cephalon.

The single available pygidium is preserved as an internal mould. The description is

partly based on a latex cast of a fragmentary counterpart external mould of the same specimen.

Pygidium wider than long. Axis with 15 rings, the last two of which are represented by aligned tubercles. Each ring with 9 to 11 tubercles arranged in longitudinal rows, median tubercles the most prominent. Ring furrows deep.

In lateral profile axis gently declining to position of sixth ring, more steeply declining thereafter. Axis stops short of posterior margin and overhangs post-axial area. Anterior axial rings inclined forward, posterior ones become progressively more backwardly inclined posteriorly.

In posterior profile axis rises high above pleural regions, semi-octagonal in cross section. Pleural field rises gently from axial furrow but is flexed strongly downward at about $\frac{2}{3}$ total width of field from axial furrow. The fulcrum is marked by a longitudinal (exs.) row of prominent tubercles.

Pleural region subdivided by ten prominent posterior pleural bands (Whittington, 1960, p. 406), the posteriormost two of which are nearly parallel to the axis. The posterior bands persist to the pygidial margin where each is represented by a marginal tubercle. The anterior pleural bands are visible only on the first five segments of the internal mould. Posterior pleural bands about twice as long (exs.) as anterior bands and more strongly convex. There are 5 to 8 evenly spaced tubercles on posterior bands 1 through 8. Interpleural furrows very faint on internal mould.

There is no border furrow, the border being set off by a change in slope.

Dimensions (in mm.)

	USNM 145307	USNM 145308	USNM 145309
cranidial length	8.0	6.9	—
glabellar length plus occip. ring	5.5	4.9	—
glabellar length to occip. furrow	4.7	4.1	—
max. glabellar width	5.0	4.0	6.3
beta-beta width of facial sutures	9.4	6.3	—
length of frontal area	2.6	2.0	—
cephalic width	(15.1)	—	(17.4)
	USNM 145310		
max. axial width	4.6		
pygidial width	12.5		
pygidial length	10.2		

Discussion. Because of the widely different ages of the Australian and Argentinian occurrences of *A. gardneri*, Campbell has proposed (Campbell and Engel 1963, p. 112) that the Argentine specimens now be assigned to a separate species. I agree with this

EXPLANATION OF PLATE 42

Australosutura aff. *A. gardneri* (Mitchell).

Figs. 1–5. Cephalon lacking the left free cheek. 1, Dorsal view ($\times 4.4$). 2, Latex cast of fragmentary counterpart mould of this specimen showing anterior branch of facial suture ($\times 6$). 3, Oblique exterior view ($\times 4.4$). 4, Lateral view ($\times 4.4$). 5, Anterior view ($\times 4.4$). USNM No. 145307.

Fig. 6. Fragmentary cephalon showing genal spine, dorsal view ($\times 4$). USNM No. 145309.

Fig. 7. Cranidium, dorsal view ($\times 5$). USNM No. 145308.

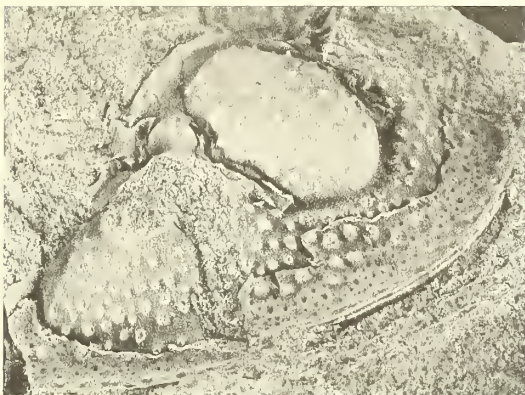
Figs. 8–9. Exfoliated pygidium. 8, Dorsal view. 9, Lateral view (both $\times 3$). USNM No. 145310.



1



2



3



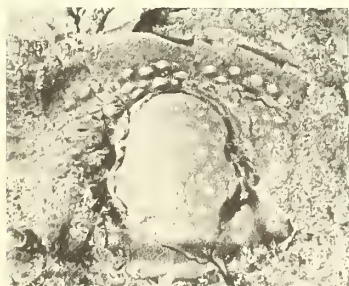
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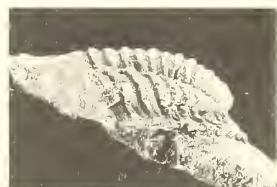
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7



8



9

suggestion but for morphologic rather than stratigraphic reasons. Several major characters which distinguish the Argentine specimens from the Australian topotypes as well as from the Oklahoma material are discussed in the foregoing section on description.

Although the Oklahoma specimens appear to differ in no important respects from the topotypes of *A. gardneri*, it is considered advisable to identify them for now as *A. aff. A. gardneri* because of their imperfectness and the fact that I have not examined the topotype specimens.

A Tournaisian species of *Australosutura* from the Tulcumba sandstone of Australia has been described as *Australosutura sp.* (Campbell and Engel 1963, p. 110). This species differs in many respects from the Oklahoma specimens. It has: (1) a distinctly longer and narrower glabella; (2) the glabella more strongly convex in transverse cross section; (3) no enlarged tubercle opposite the 2p glabellar furrow; (4) a relatively shorter, broader pygidium; and (5) the inner part of the pygidial pleural fields much flatter in cross section.

The similarities between *Australosutura* and *Cordania* have already been pointed out (Amos, Campbell, and Goldring 1960, p. 229), and *Cordania* has been suggested by those authors (op. cit. p. 230) as a possible ancestor of *Australosutura*. I would suggest that *Mystrocephala* Whittington (1960, p. 413) in having a broad, concave preglabellar field; no broad, convex cephalic border; and the posterior pygidial segmentation represented by posterior pleural bands is even closer to *Australosutura* than is *Cordania*. *Mystrocephala* is also closer in age to *Australosutura*. The youngest representatives of *Mystrocephala* are Givetian in age (Whittington 1960, p. 414), whereas *Cordania* does not occur in beds younger than Lower Devonian (op. cit. p. 409). Thus *Mystrocephala* is better qualified than *Cordania* as a possible ancestor of *Australosutura*.

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DESCRIPTIONS OF SCHIZAEACEOUS SPORES TAKEN FROM EARLY CRETACEOUS MACROFOSSILS

by N. F. HUGHES and JUDITH MOODY-STUART

ABSTRACT. Full descriptions are given of spores taken from the original macrofossil material of *Ruffordia goepperti* (Dunk.), *Pelletieria valdensis* Seward, and *Schizaeopsis americana* Berry. All three plants are of Early Cretaceous age, the first two from the Lower Wealden of England, and the last from the Patuxent Formation of the Potomac Group of Virginia, U.S.A. The use of measurements in the erection of species in the dispersed spore genus *Cicatricosisporites* is discussed in the light of these observations.

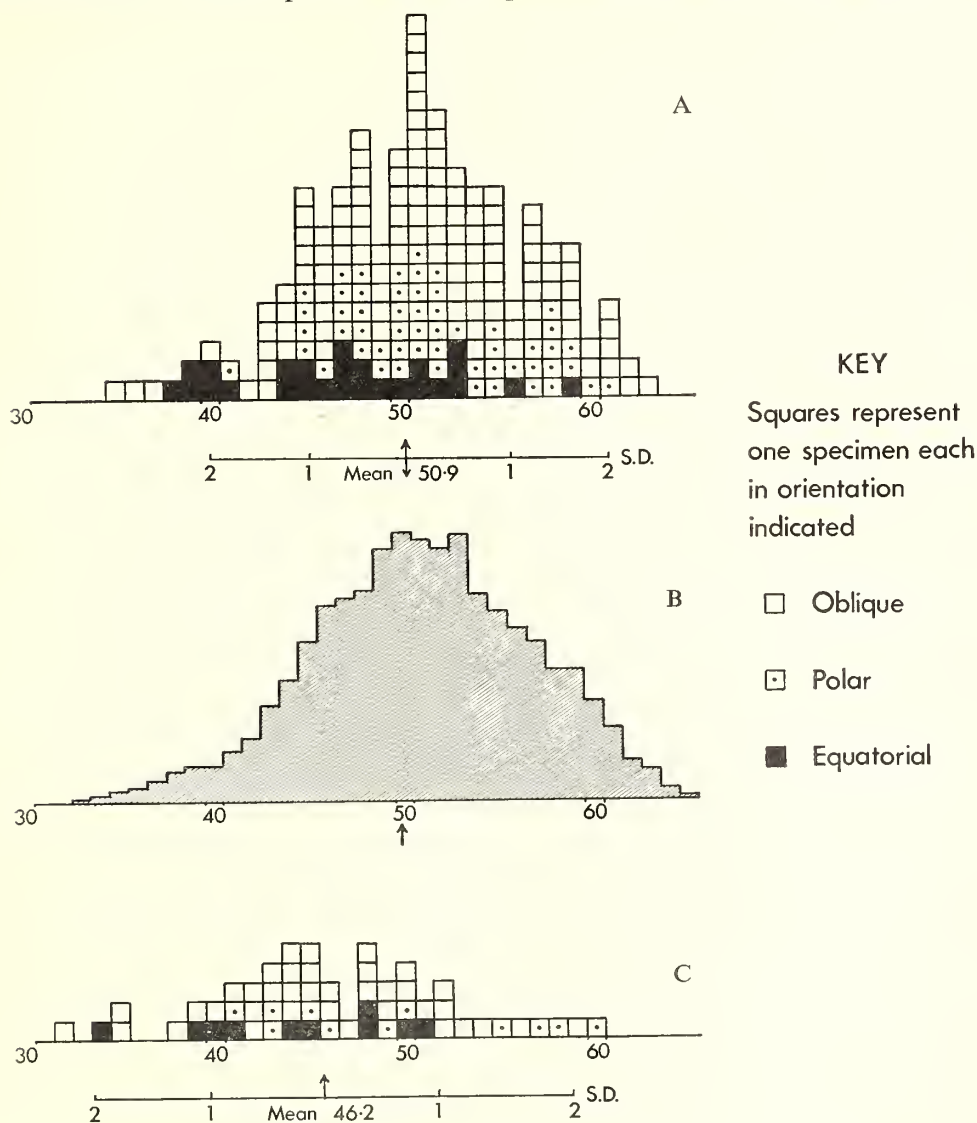
DISPERSED spore palynological studies show that the spore type usually classified as *Cicatricosisporites* Pot. and Gell. first appears in the Early Cretaceous or latest Jurassic, and then diversifies rapidly. Unfortunately these spores have not yet proved to be of great stratigraphical value in the Cretaceous period, and we think this is almost entirely due to the effects of poor typification and description, and of uncoordinated nomenclature. Bolkhovitina (1961) has brought together most of the fossil records of this group in a very useful paper, although her system of nomenclature is unfortunate and many of the figures of other authors which she was obliged to reproduce were inadequate in their original form.

It so happens that three separate fertile plant organ species, believed to belong to the Schizaeaceae, were described with their spores in the period 1911–13. The illustrations of the spores were generalized sketches, with in two cases rather inadequate photographs; and the descriptions do little more than allude to the probable fern family affinity, a treatment which was no doubt considered adequate at the time. Couper (1958) published some photographs of spores of *Ruffordia goepperti* which had been known previously only from Seward's (1913) sketch, but Couper regarded these spores as comparable with his dispersed spore material which he placed in the Eocene species *Cicatricosisporites dorogensis*. As far as we know neither the spores of *Pelletieria valdensis* nor of *Schizaeopsis americana* have been adequately described.

All the material of *Ruffordia* and *Pelletieria* has been kindly loaned for the purpose by the Department of Palaeontology, British Museum (Natural History). The necessary pull from the *Schizaeopsis* specimen was taken during a visit (N.F.H. July 1959) to the United States National Museum, Washington, and permission to figure the material was kindly given later by Dr. F. M. Hueber of that institution. The relevant slide preparations will be sent to the institutions concerned. Potonié (1965, pp. 45–46) refers to this same material which he examined when in Cambridge.

Preparations were made by brief oxidation (approx. two hours) in concentrated nitric acid only, clearance in approx. 5 per cent. ammonia, and mounting unstained in glycerine jelly. In each case all of the material removed from the plant was mounted; it was handled only by pipette and was not centrifuged. Specimens recorded were all

those present on certain selected traverses on the slide preparation. Stage co-ordinates refer to Ortholux microscope no. 491249, Department of Geology, Cambridge.



TEXT-FIG. 1. Frequency distribution histograms of maximum diameter in microns of spores of *Ruffordia goepperti*. A, New preparation (V2192b-f), 200 specimens; standard deviation 5.2μ , coefficient of variation 10 per cent. B, Five point moving average from the data of A. C, Seward's preparation (V2192a), 58 specimens (all available); standard deviation 6.1μ , coefficient of variation 13 per cent.

DESCRIPTIONS

Family SCHIZAEACEAE

Genus RUFFORDIA Seward 1894

Type species. *Sphenopteris goepperti* Dunker 1846 (Dunker's earlier reference not effective).

Remarks. Although the genus *Ruffordia* was well conceived, Seward should have erected a new species for his relatively good fertile material, instead of relying on the inadequately described holotype (sterile frond) of Dunker. In view of the remarks of Michael (1936, p. 34) a new species may still be necessary, as she could not find in the German specimens the variability which Seward reported. Nomenclatural difficulties would result from any such change now.

Ruffordia goepperti (Dunk.) Seward 1894 (spores)

Plate 43, figs. 1–12

- 1913 Seward, p. 91, text-fig. 2A.
 non 1921 Halle, p. 11, pl. 2, fig. 8.
 1958 Couper, p. 109, pl. 17, figs. 4–6.
 1962 Potonić, p. 104, pl. 10, fig. 268.

Holotype. We have located and figured (Pl. 43, fig. 10) a spore on Seward's slide V2192a which by elimination appears to be the original of his text-fig. 2A (1913); we are considering this spore to be the holotype. Seward's preparation and mounting methods for this material are not known, and the spore is now very pale in colour. The size range and mean of the fifty-eight specimens on his slide differ from those of our preparation (see text-fig. 1c). The spore figured by Couper (1958, pl. 17, figs. 4, 5) is probably another specimen nearby on the slide (OR 48.1 126.1).

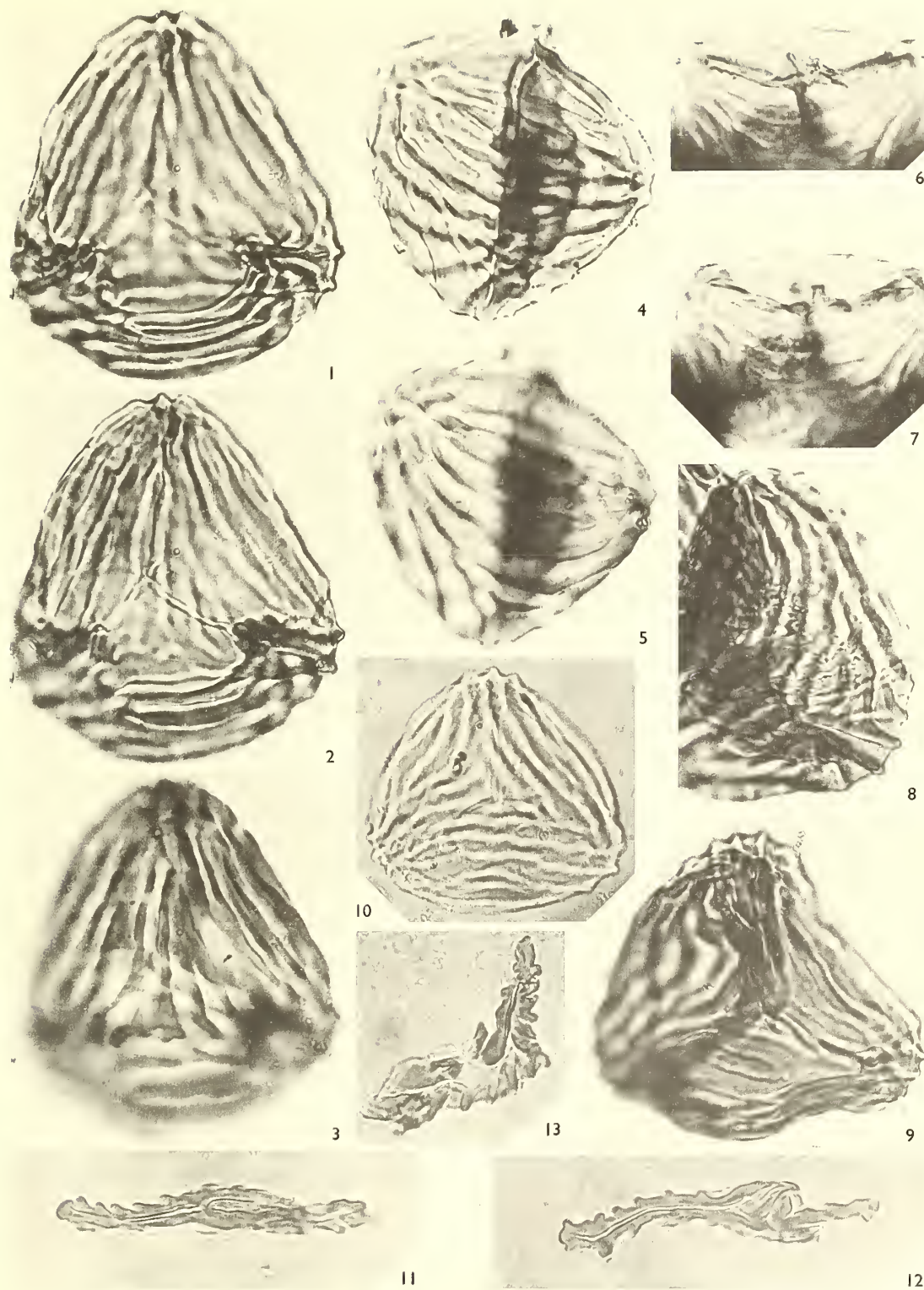
Locality. The specimen V2192a is clearly marked Rufford Collection, Ecclesbourne, nr. Hastings, in spite of Seward's (1913, p. 91) record of Fairlight. The rock is a hard red-brown sideritic siltstone of maximum grain size $50\ \mu$. It is likely to have come from the base of the Ashdown Sands or from the top of Fairlight Clay division *e*.

Material. Spores were taken by needle and by 'pull' from what appeared to be sporangia on the middle section of the frond of specimen V2192a, which according to Museum labels in Seward's handwriting was the specimen he used but did not specifically cite (1913) in making his slide (now V2192a).

Emended spore diagnosis. Spores trilete tetrahedral with strongly convex distal surface, but with rounded triangular amb. Contact faces smooth (Pl. 43, figs. 1–2). The lips are simple membraneous $2\text{--}3\ \mu$ high extensions of the exine (Pl. 43, fig. 6) which has a constant thickness of $1.5\ \mu$ excluding sculpture. The inter-radial equatorial and distal regions bear three sets of sub-parallel muri which occasionally join to form a partial reticulum (Pl. 43, figs. 4, 5, 8). The three sets of muri leave a triangle (Pl. 43, fig. 10) of varying size centred on the distal pole, with variable sub-parallel sculpture within the triangle. Muri, of rounded profile, $1.5\text{--}2.0\ \mu$ high and wide, spaced on average

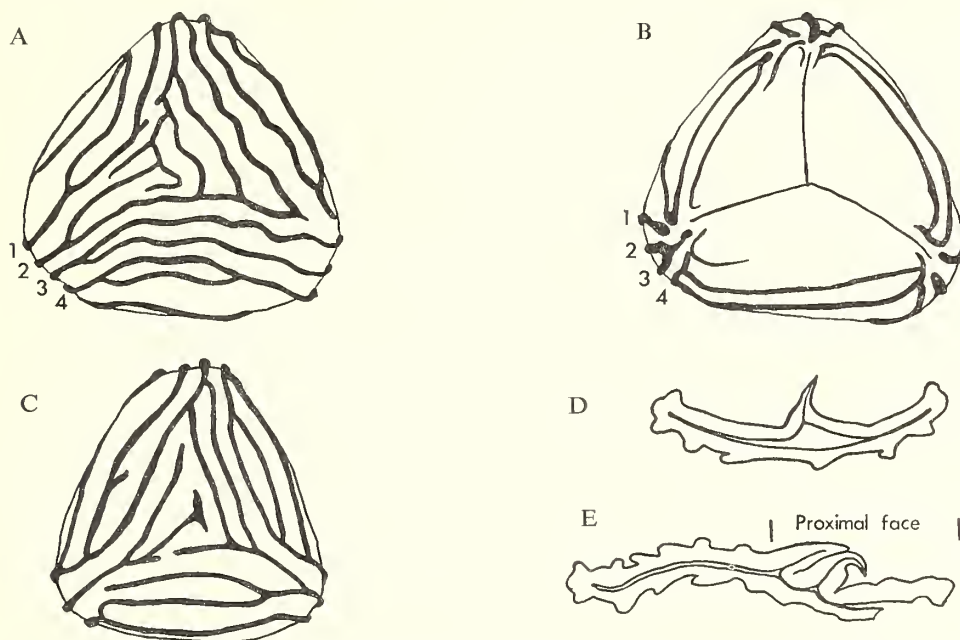
EXPLANATION OF PLATE 43

Figs. 1–12. *Ruffordia goepperti* (Dunk.) Seward; spores taken from specimen V2192a BMNH, $\times 1000$. 1–3, Proximal aspect, high, mid and low focus respectively; prep. V2192c, OR 33.5 108.5. 4–5, Equatorial aspect, mid and low focus; prep. V2192d OR 30.9 120.6. 6–7, Oblique proximal aspect, mid and high focus; Prep. V2192d, OR 32.2 120.3. 8, Oblique aspect pattern of distal muri; prep. V2192c, OR 46.4 117.9. 9, Proximal aspect, showing radial rib profile formerly diagnostic; prep. V2192c, OR 46.4 112.4. 10, Holotype, proximal aspect, low focus (distal); Seward's prep. V2192a, OR 48.2, 127.2. 11, Section perpendicular to polar axis, triplan, distal; prep. V2192g, OR 54 112.4. 12, Adjacent section, showing laesura with compressed lips and proximal face; prep. V2192g, OR 60.1 115.6. 13, Section parallel to polar axis, laesura open; prep. V2192h, OR 40.1 125.1.



2–3 μ apart (Pl. 43, fig. 8). Muri of adjacent sets do not coalesce (see text-fig. 2A–C) in equatorial radial regions which are flexible and not thickened.

Dimensions. Diameter (200 specimens) 35–(51)–63 μ (preparations V2192b–f); 80 per cent. of specimens fall between 44 and 58 μ . Percentage of specimens in polar view 28, equatorial view 13, and oblique 59 as plotted in text-fig. 1A. Similar observations for Seward's slide V2192a are given in text-fig. 1C; the lower values for diameter (58 specimens) 32–(46)–58 μ , 80 per cent. between 39 and 55 μ , may be due to difference in maceration procedure.



TEXT-FIG. 2. *Ruffordia goepperti* (spores), diagrams $\times 1000$; muri shown in black. A–C, from Seward's preparation (V2192a) to illustrate the configuration of the muri. A, Distal; B, Proximal faces of holotype, Plate 43, fig. 10, OR 48.2 127.2. C, Distal face of specimen figured by Couper (1958), OR 48.1 126.1. D, Section normal to laesura, half radial distance from pole, showing concave proximal face and false margo. E, Specimen of Plate 43, fig. 12, showing folded proximal face and false margo.

Description. All spores are strongly compressed and usually folded. Possibly because they were dried out before burial and became concave proximally, there is a tendency for the parts of the exine adjacent to the laesurae to be pressed together; this raises the lips, simulates a margo in some specimens, and causes some proximal rigidity (text-fig. 2A; Pl. 43, figs. 6, 12, 13). The arrangement of muri in the radial region is comparable with that shown by Dettmann (1963, text-fig. 4p); the mode of preservation however, always causes difficulty in observing details of the radial areas.

Comparison. The spores obtained from *R. goepperti* (Halle 1921) from an unspecified horizon in Ussuri appear from poor illustrations to be of a different type.

Remarks. Groot and Penny (1960) combined the spores of Seward and Couper in the dispersed spore genus *Cicatricosisporites*. Bolkhovitina (1961) erected *Ruffordia aralica*

for dispersed spores which have widely spaced high muri but differ from spores of *R. goepperti* in overall smaller numbers of muri. Brenner (1963) placed all these spores in synonymy in *Cicatricosisporites aralica* comb. nov., but none of this procedure is admissible.

Genus PELLETIERIA Seward 1913

Remarks. The available material of the single macrofossil species *P. valdensis* is more extensive than that figured by Seward, but the necessary re-description cannot be included in this paper. We assume that Seward intended the specimen V2329 (pl. XII, fig. 12a) to be the holotype and herewith designate it as such in case there is any doubt. The specimen of plate XII, fig. 12b is on V2329 but has been partly destroyed in extracting spores, presumably by Seward; on the same rock specimen are the originals of Seward's text-fig. 4A and G but 4B-E have not been located. The specimen of text-fig. 4F (now damaged) is on slide V2329b; that of text-fig. 3B is on V2368, text-fig. 3A on V51843, and text-fig. 3C on V51840.

Pelletieria valdensis Seward 1913 (spores)

Plate 44, figs. 1-8; Plate 45, figs. 1-7

1913 Seward, p. 91, pl. 14 fig. 5, text-fig. 2B.

Holotype. Although Seward's wording (1913, p. 92, para. 2) may be taken to suggest that the specimen of his text-fig. 3B (V2368—Rufford Coll.) provided the spores, it seems certain from all other evidence that they came from V2329. We have found the original of Seward's photograph (1913, pl. 14, fig. 5) on slide V2329a and we re-figure it as the holotype (Pl. 44, fig. 4). It has not been possible to identify the obliquely viewed specimen of Seward's text-fig. 3B.

Locus typicus. V2329 and V2368 are both labelled Ecclesbourne, nr. Hastings; V2329 is a coarse grey siltstone, unbedded, with maximum grain size 150 μ . These specimens must again come from the lowest Ashdown sand or Fairlight clay *e*.

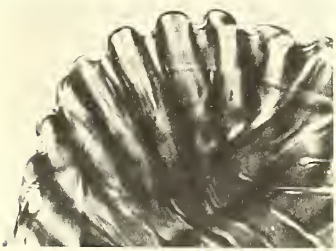
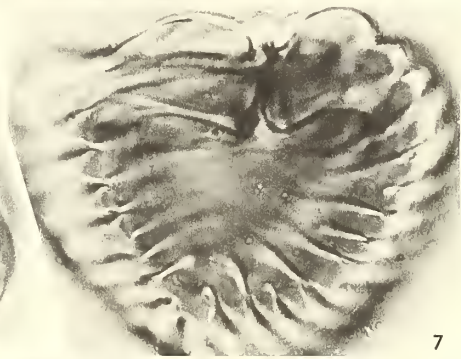
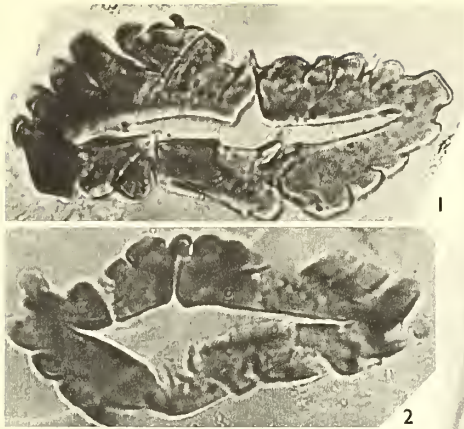
Material. Additional spores were taken from V2329 from an isolated spore mass very close to the original of plate XII, fig. 12b (Seward 1913).

EXPLANATION OF PLATE 44

Figs. 1-8. *Pelletieria valdensis* Seward; spores taken from specimen V2329 BMNH, $\times 1000$. 1-2, Sections parallel to polar axis, through laesura (2, near outer termination of laesura); prep. V2329j, OR 33.3 119.9 and 31.5 114. 3, Distal aspect, high focus; prep. V2329i, OR 37.8 117.6. 4, Holotype, proximal aspect; Seward's prep. V2329a, OR 28.7 118.9. 5-6, Equatorial aspects, prep. V2329f. 5, Showing profile of muri; OR 42.6 117.9. 6, Laesura open; OR 35.3 115.3. 7, Small specimen, equatorial aspect with optical section of proximal exine; prep. V2329a, OR 38.7 125.8. 8, Equatorial aspect; prep. V2329h, OR 35.7 117.8.

EXPLANATION OF PLATE 45

Figs. 1-7. *Pelletieria valdensis* Seward; spores taken from specimen, V2329 BMNH, $\times 1000$. 1-2, Sections perpendicular to polar axis; prep. V2329j, OR 29.4 113.9 and OR 51.5 107.7. 1, Distal (slightly oblique). 2, Proximal face showing depression bordering laesurae. 3, Proximal aspect, high focus; prep. V2329g, OR 47.8 118.7. 4, Distal aspect; prep. V2329g, OR 40.7 121.7. 5-7, Sections parallel to polar axis; prep. V2329l, OR 50 111.8, OR 45 112.5, OR 42.3 112.3.



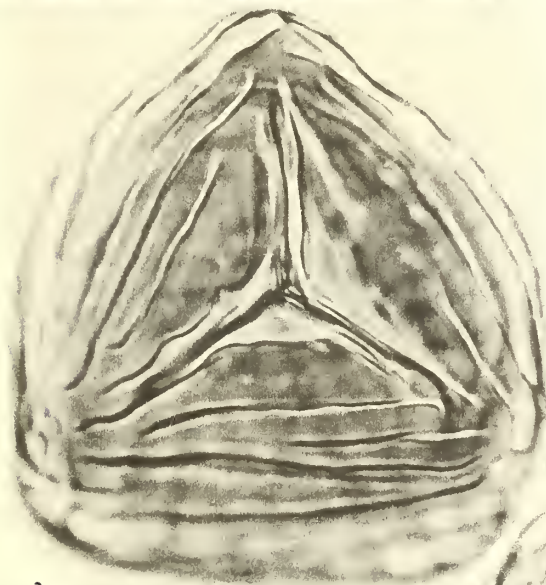
HUGHES and MOODY-STUART, Lower Cretaceous spores



1



2



3



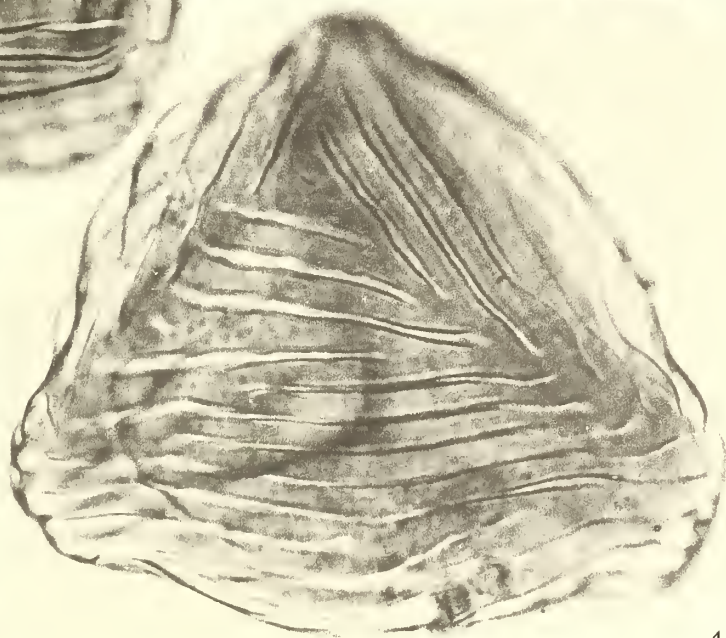
5



6

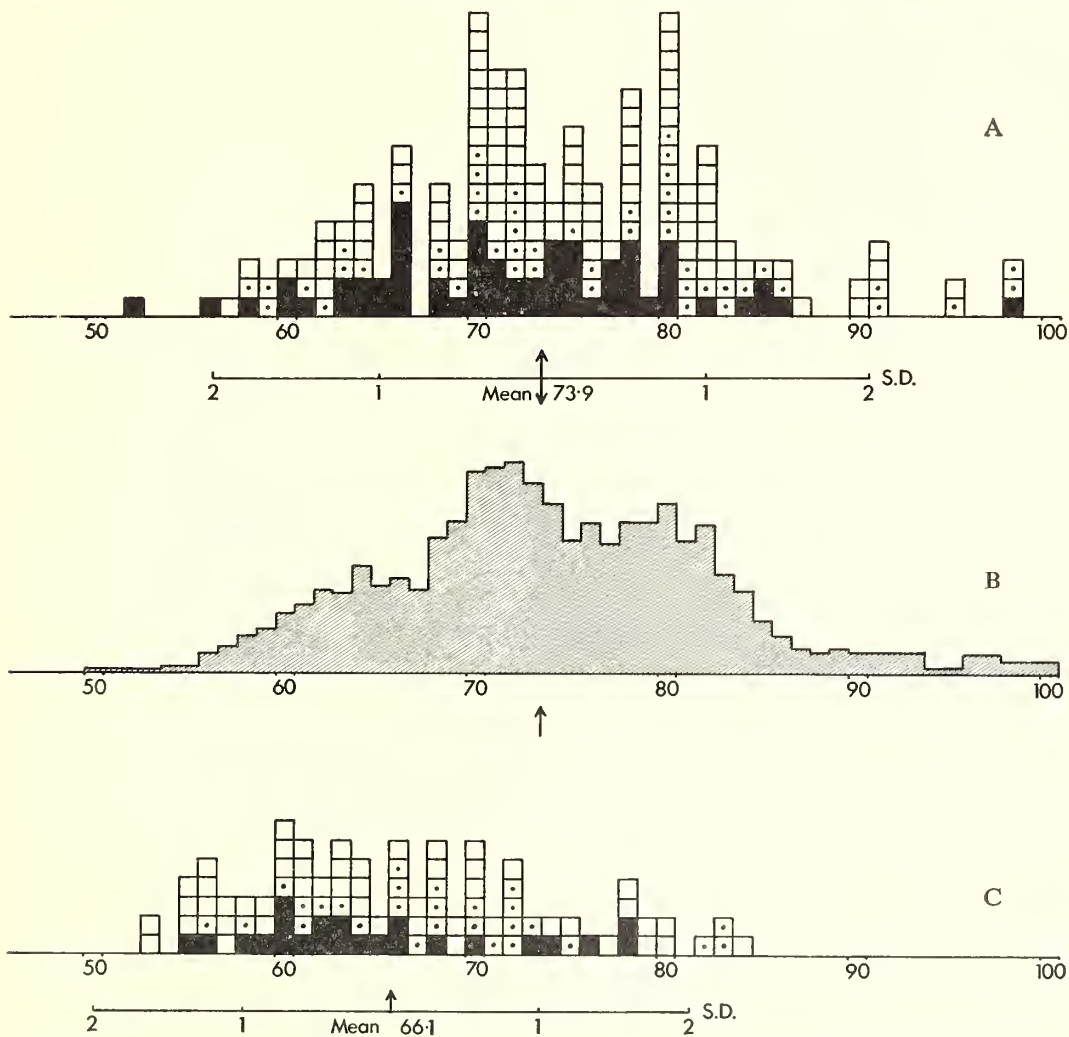


7



4

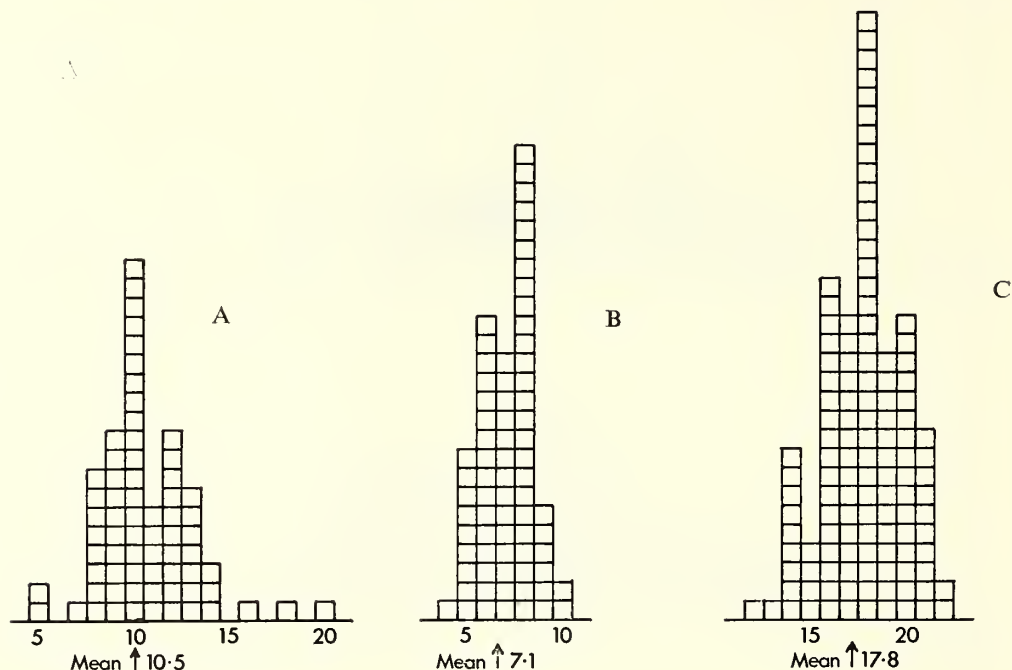
Emended diagnosis. Trilete spores with rounded triangular amb. Laesurae simple and with thin lips, of medium length flanked by variably deep and narrow areas of negative sculpture. Proximal and distal surfaces bear a regular canaliculate sculpture, best



TEXT-FIG. 3. Frequency distribution histograms of maximum diameters in microns, of spores of *Pelletiera valdensis*. A, New preparation (V2329f), 200 specimens; standard deviation 8.5μ , coefficient of variation 12 per cent. B, Five point moving average from the data of A. C, Seward's preparation (V2329a), 100 specimens; standard deviation 7.7μ , coefficient of variation 12 per cent.

described as of lumina 0.5 to 1.0μ wide and 4μ apart. The lumina, in three parallel inter-radial sets, do not coalesce but merely inter-finger in the radial regions, maintaining the latter as more rigid areas which affect the shape of the spore. Inter-radial exine thickness 6.5μ .

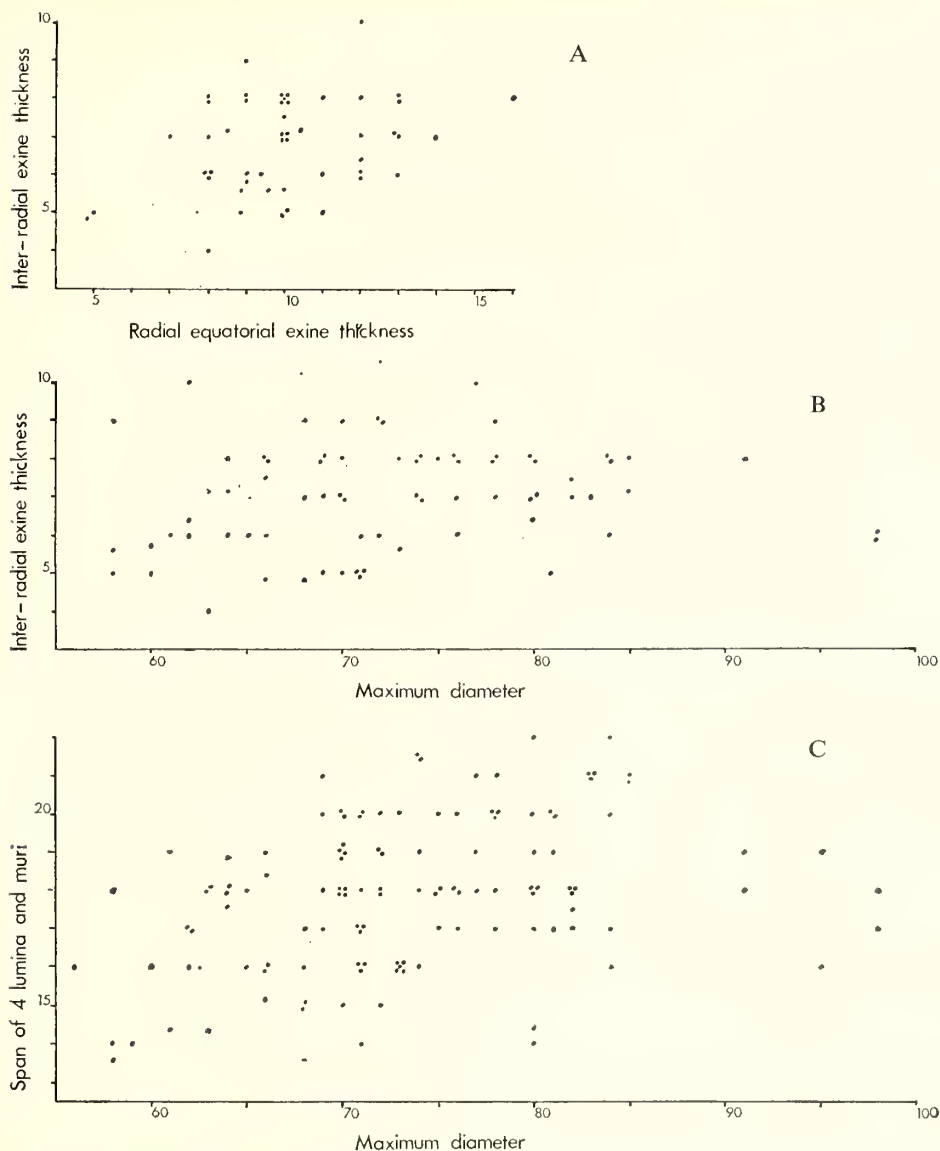
Dimensions. Diameter (200 specimens) 52–(74)–98 μ (new preparation V2329f); 80 per cent. of specimens have maximum diameter between 63 and 84 μ (text-fig. 3A). Specimens in polar aspect 25 per cent., equatorial aspect 30 per cent. Similar observations on 100 specimens from Seward's slide V2329a give diameter 53–(66)–84 μ (text-fig. 3C); 80 per cent. of values fall between 56 and 78 μ . Specimens in polar aspect 26 per cent., equatorial aspect 23 per cent. Values for Seward's specimens are again lower (see under *Ruffordia*).



TEXT-FIG. 4. Spores of *Pelletieria valdensis*; distribution histograms of measurements in microns with one square per specimen. Total numbers of specimens differ as not all characters are observable on every spore. A, Observed thickness of exine in radial equatorial region, 69 specimens. B, Inter-radial exine thickness, 73 specimens. C, Span covered by four lumina (and four muri), 123 specimens.

Description. The symmetry of the distal sculpture varies from the extreme seen in 24 per cent. of the specimens in which the triangle is centred on the distal pole (Pl. 45, fig. 4), through various intermediates to the sub-parallel lumina of Plate 44, fig. 3; it is doubtful whether this feature can have the taxonomic significance implied by Deak (1963). The span covered by four lumina (the same as the usual four muri) is recorded on text-fig. 4C, and plotted on text-fig. 5C. The resulting muri can be described as typically 3–(4)–5 μ wide, 3–4 μ high and flat-topped. The inter-radial exine thickness is recorded (text-fig. 4B) and plotted (text-fig. 5); such variability is of course much more easily observed in a thick exine such as in *Pelletienia*, than in one near the limit of optical resolution. The measured radial and inter-radial variable exine thickness depends on the degree to which the lumina are 'open' and this is affected by:

1. The directions of the lumina with respect to the amb (contrast Pl. 44, fig. 5, with a section, Pl. 45, fig. 7).

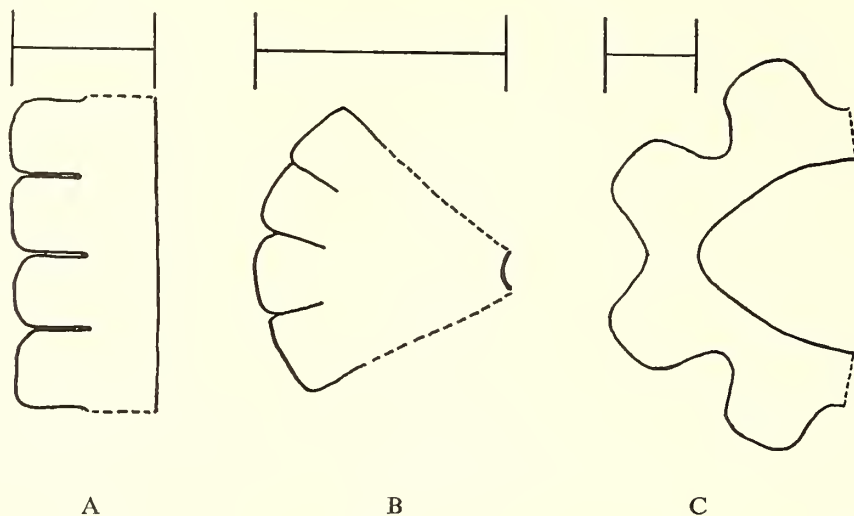


TEXT-FIG. 5A-C. *Pelletieria valdensis*; linear plots showing the possible relationships between some of the characters recorded in text-figs. 3 and 4, scales in microns.

2. The distance of the measurement from the radial areas where the lumina close; thus the diameter of the spore will affect this especially in small specimens.
3. The degree of inflation (in life?), and the compression of the specimen (in diagenesis).

On average (text-figs. 4, 5A) the radial thickness is fifty per cent. greater than the inter-radial. The opening of lumina up to an observed maximum of 90° is calculated to reduce

to two-thirds the depth of a lumen (text-fig. 6A, C), but this reduction will not explain the observed differences in exine measurements on many specimens. The simplest assumption is that the exine suffers some distortion but no change of volume when it is folded; the scale diagrams of text-fig. 6B-C show observed extremes of exine profile and measurements; compare with Plate 45, fig. 4. Text-fig. 6A compares with exine seen unfolded in Plate 45, fig. 7. By drawing on graph paper it was shown that all three



TEXT-FIG. 6. *Pelletieria valdensis*; diagrams of sections ($\times 2000$) of spore exine to explain variable exine thickness, bars show exine thickness as would be measured by optical section in polar view. A, Inter-radial exine, not folded; sections normal to direction of lumina. B-C, Exine folded at amb; plane of section containing polar axis. B, Radial. C, Inter-radial.

diagrams have the same cross-sectional area. Since this area is taken normal to the plane of folding (in text-fig. 6B, C), it will be proportional to the volume of a parallel element of exine. The observed differential exine thickness may be explained thus without postulating a taxonomically significant radial thickening. Since the orientation of the lumina affects the spatial properties of the spore, any asymmetry in the distal sculpture (76 per cent. of the specimens) often causes irregularity in the amb and in the exine measurements.

The tapering lips project above normal exine level near the proximal pole only; they are flanked by a variable negative area which closes or coalesces with a lumen when the lip membrane merges into the exine at the apparent limit of a laesura. We suggest that the negative sculpture, often deeper than a lumen, gives flexibility to an otherwise rigid proximal face. From Plate 45, figs. 2 and 5, and Plate 44, fig. 2, it can be seen that the laesurae extend lipless almost to the equator, well beyond what appears to be the limit in proximal surface view.

Comparison. Couper (1958) suggested that these spores were similar to his dispersed spore species *Cicatricosisporites dorogensis* but the size range and other features are

entirely different. A distinction is more necessary between this spore and *C. brevislaesuratus* Couper (type from Barremian/Aptian) which is even larger ($90\ \mu$) and is described as having an unsculptured contact face. Bolkhovitina (1961), perhaps on account of Couper's comparison, has inadvisedly (and wrongly) placed a number of unrelated dispersed spore species in this macrofossil genus.

The spores described from the Hastings Beds by Boodle (1895) were similar to those of *P. valdensis*; they occurred in a large spore mass but their provenance was not discovered.

Botanical Affinity. Neither the macrofossil remains nor the spores of *Pelletieria* are very close in detail to species of *Ceratopteris*, although the suggestion that the macrofossil may have been a water plant and not necessarily related to normal Schizaeaceae is worth exploring.

Genus SCHIZAEOPSIS Berry 1911b

Remarks. The genus is only valid from Berry's second paper (1911b), when he erected the necessary new species for the single specimen concerned (now USNM 3209).

Schizaeopsis americana Berry 1911 (spores)

Plate 46, figs. 1–8; Plate 47, figs. 1–10

1911a Berry, p. 193, pl. 12, figs. 2–6.

1911b Berry, p. 216, pl. 22, figs. 4–9.

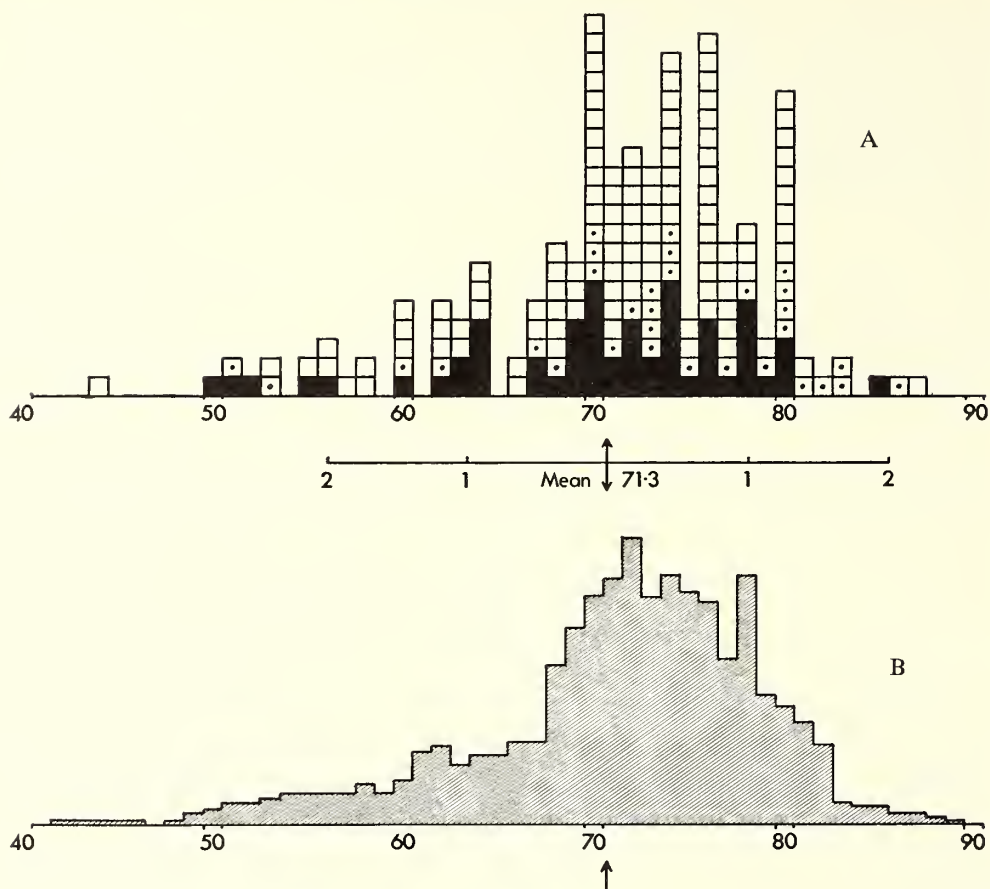
Holotype. The original single photograph (Berry 1911b, pl. 22, fig. 4) is not recognizable; the drawings (pl. 22, figs. 5–9) are too generalized to be used further.

Locus typicus. Patuxent formation, Fredericksburg, Virginia, U.S.A.

Material. The rock specimen (USNM 3209) is a medium brown non-calcareous siltstone with plant fragments and the fairly large fertile frond described by Berry (1911b, pl. 22, figs. 1–3). A small part of the spore mass was taken from the tip of one of the central leaf lobes of the specimen; preparations USNM 3209 g–j.

Emended diagnosis. Spores almost spherical; amb convex rounded triangular. Laesurae trilete, short, simple, with raised thin ($0.5\ \mu$) lips. Whole surface covered by uniform narrow muri $1\frac{1}{2}\ \mu$ wide, $1\ \mu$ high, flat-topped; lumina $1\ \mu$ wide. The whole proximal face is covered by three inter-radial sets of muri; the equatorial region bears a single set of five or six circular muri parallel with the outer members of the proximal inter-radial sets. The distal surface is covered by a single set of parallel muri which converge abruptly opposite two radial areas and swing round parallel to the equatorial set in the third. Exine thickness $3\text{--}4\ \mu$ in distal and equatorial regions, thicker immediately round laesurae as a margo (*sensu* Harris 1955, p. 26).

Dimensions. Diameter (200 specimens) $44\text{--}(71)\text{--}87\ \mu$ (preparations USNM 3209 g–j); 80 per cent. of specimens have maximum diameter between $61\ \mu$ and $80\ \mu$. Specimens in polar aspect 16 per cent., equatorial 28 per cent. The records on text-fig. 7A, which are plotted on text-fig. 8A–C, show a numerically small but statistically significant group of small spores in this preparation. The group was distinguishable by eye, and proves to consist of small spores with thicker distal exines and narrower muri and lumina which had never opened at the laesurae (Pl. 46, figs. 5, 6).



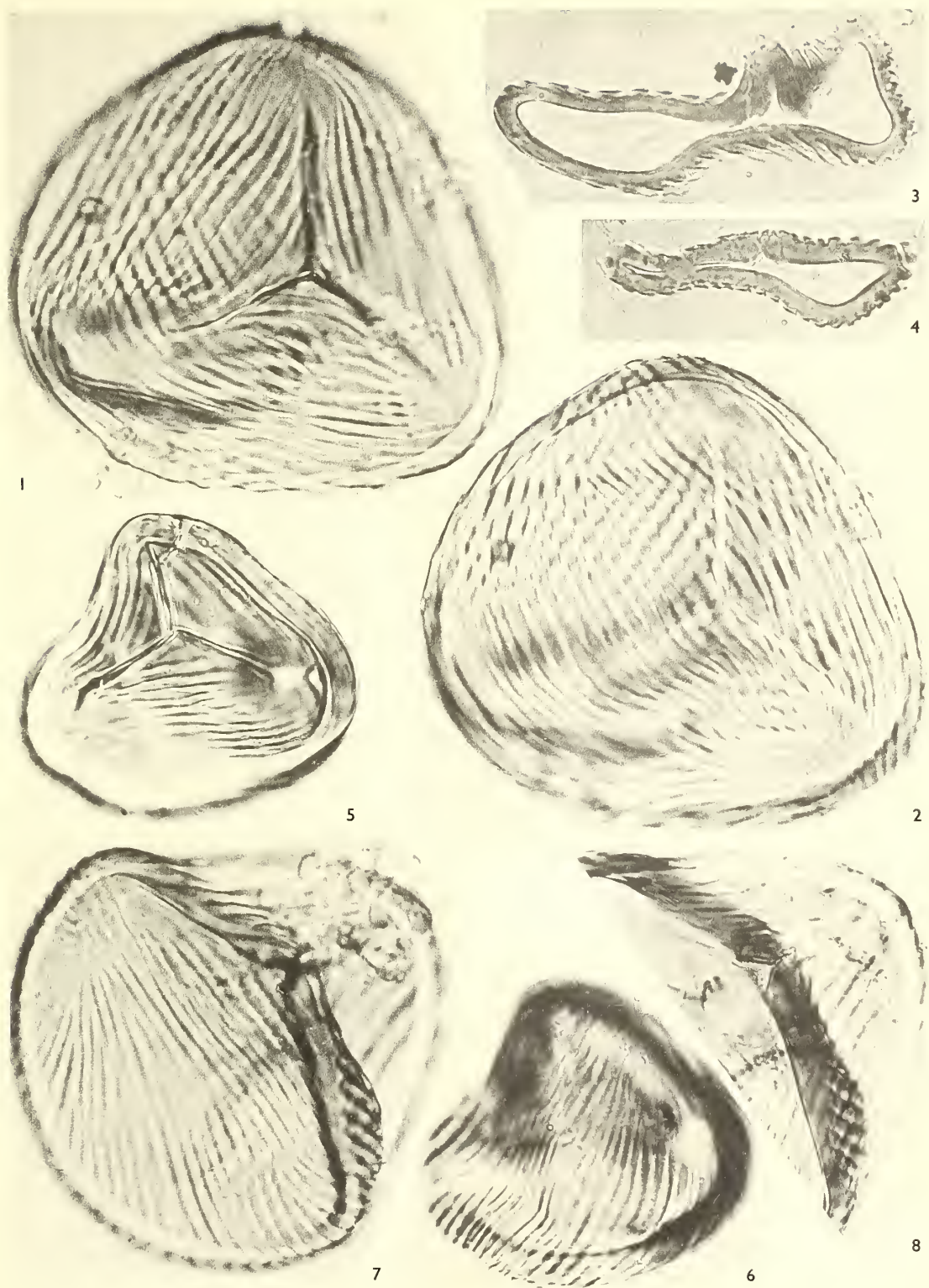
TEXT-FIG. 7. Frequency distribution histograms of maximum diameters in microns of spores of *Schizaeopsis americana*. A, New preparations (USNM 3209 *g-j*), 200 specimens; standard deviation 7.4μ , coefficient of variation 10 per cent. B, Five point moving average from data of A.

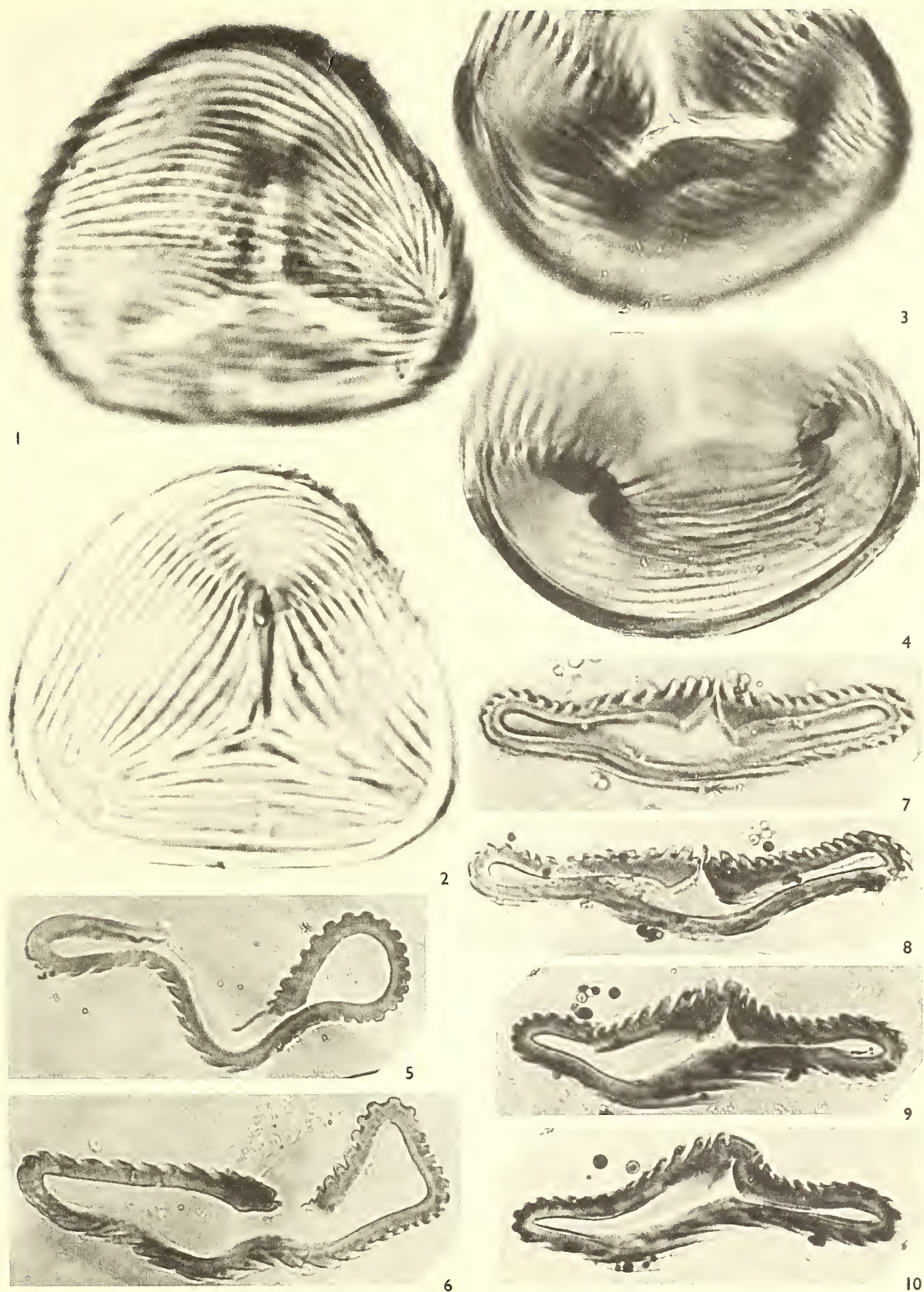
EXPLANATION OF PLATE 46

Figs. 1-6 *Schizaeopsis americana* Berry; spores ($\times 1000$) taken from specimen USNM 3209; each preparation bears this number with the suffix here indicated. 1-2, Proximal aspect, mid and low focus respectively; prep. *g*, OR 36.9 118. 3, Section parallel to polar axis, at end of laesura; prep. *l*, OR 22.2 119.5. 4, Similar section, just beyond laesura; prep. *k*, OR 39.6 109.2. 5-6, Proximal aspect, small specimen, mid and low focus; prep. *j*, OR 34.3 118.5. 7-8, Oblique aspect, high focus and optical section through laesura; prep. *h*, OR 34.6 125.5.

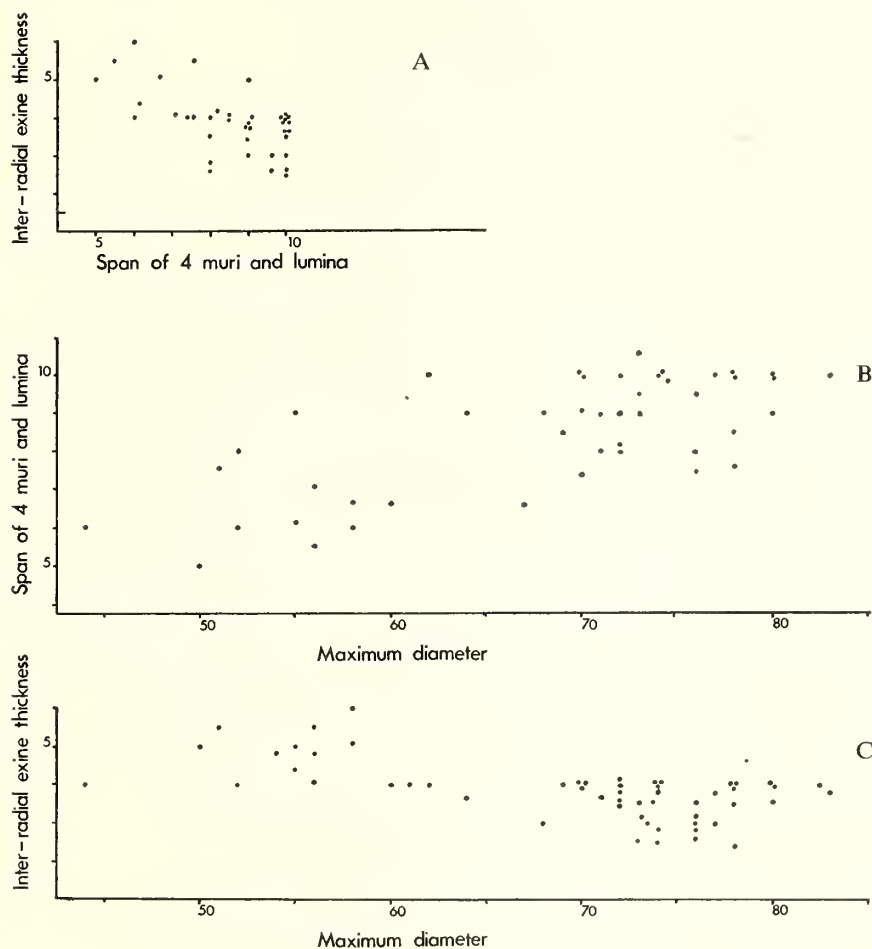
EXPLANATION OF PLATE 47

Figs. 1-10. *Schizaeopsis americana* Berry; spores ($\times 1000$) taken from specimen USNM 3209; each preparation bears this number with the suffix here indicated. 1-2, Proximal aspect, low and mid focus; prep. *h*, OR 34.9 120.7. 3-4, Proximal aspect, spore expanded showing lips (see text-fig. 10D), mid and high focus; prep. *i*, OR 36.2 123.6. 5-6, Sections parallel to polar axis, open laesura; prep. *l*, OR 40.4 119.6 and OR 27.5 120.4. 7-10, Successive sections parallel to polar axis, across laesura; prep. *m*, OR 24.2 109.7, OR 37.3 108.9, OR 28.6 109.5, and OR 31.0 109.8.





Description. Text-fig. 9A-C shows in diagrammatic section various states of the laesura and margo as seen in normal spores (Pl. 46, fig. 8; Pl. 47, figs. 7-8). These observed conditions may be understood as successive states on the model of an inelastic inner layer of exine bound to an outer flexible sculptured layer, the whole spore gradually



TEXT-FIG. 8A-C. *Schizaeopsis americana*; linear plots showing the possible relationships between the characters indicated, on 38, 45, and 55 specimens respectively, scales in microns.

inflating. First the lower exine pulls apart at the laesura, then the upper exine parts, and finally only the lips remain in contact.

The specimen in Plate 47, figs. 3-4, which is apparently dehiscent, shows on fuller examination closed laesurae at the bottom of a 10μ wide infolding of the proximal exine. Our explanation is that text-fig. 9D shows the effect of deflation, perhaps on drying out, on a spore which on the plant had reached the condition of text-fig. 9C. In surface view this may give the appearance of muri truncated at high angles by the laesurae.

In these spores, as in *Pelletieria*, the laesurae and margo extend beyond the apparent limit as seen in polar view (Pl. 46, fig. 4; Pl. 47, figs. 9–10).

Comparison. Berry's (1911) figures (drawings) were inadequate, and Potonié (1962, pl. 10, fig. 270) unfortunately increased the confusion with a bad re-drawing. The diameter was imprecisely quoted by Berry as 100μ , and this perhaps led Couper (1958, p. 110) into comparing these spores with his large but quite different (wide muri)



TEXT-FIG. 9. Diagrammatic sections ($\times 1000$) of *Schizaeopsis* spores, parallel to a polar axis, normal to a laesura. A–C, Successive states during inflation of the spore. D, Probable effect of subsequent deflation of a mature spore (as in drying out).

Cicatricosisporites brevilaesuratus. Brenner (1963) perpetuates this error, while his *C. potomacensis* (pl. 9, figs. 4, 5) probably is very close to *Schizaeopsis americana*. Groot and Penny (1960) do not record such a spore, but Stover (1964) figures (pl. 1, fig. 20) as *C. dorogensis*, a spore from the Arundel formation which again appears to be very close to *S. americana*.

Remarks. Although the true nature of this spore was concealed by the early description, the spore-masses and leaf were well illustrated by Berry (1911 a, b).

Validity of name. Berry (1911b, p. 219) made taxonomic and nomenclatural changes in erecting *Schizaeopsis americana* which may be suspect. We have followed his usage because (a) Berry's description is valuable while in this case Fontaine's is not, (b) Berry's work has not been challenged and has been much quoted, and (c) Berry did amplify the description of *Acrostichopteris expansa* (Fontaine), the material of which is not fertile. We feel that it is just about possible to justify Berry's procedure because no type specimens were designated by Fontaine or by others before 1911, and that therefore on balance it is simpler and more helpful to allow it to stand.

GENERAL MORPHOLOGY OF SCHIZAEACEOUS SPORES

Detailed observation of (a) the pattern of junction of muri or lumina in the radial areas, (b) the margin of the laesurae, and (c) the shape, spacing, and orientation of the muri, together provide more characters than are available in other fossil trilete fern spores. The sculptural configuration has diagnostic qualities at a species level, but the distal pattern of muri can vary if one adjacent set is under- or over-'developed' in number, and we do not believe that patterns 2 and 3 of Deak (1963, pl. 1) are fundamentally different. The features mentioned in the first sentence of this paragraph determine the flexibility of a specimen; the three spore species illustrated in this paper must differ strikingly in this original property and thus in their tendency to fold in diagenesis. Their attitude, however, under the partial compression in the sporangia or attached spore-masses will have been random, and not subject to sedimentation factors as are dispersed spores.

MEASUREMENT

Since the wavelength of light makes diffraction effects dominant below one micron, we have omitted the possible inner layering of the *Schizaeopsis* exine from diagnosis pending examination by electron micrographs.

We have chosen 'maximum diameter' as a principal measurement because it was obtainable from all specimens, and in equatorial views it was measured along the equator. It can be seen from text-fig. 1A that equatorial views of *Ruffordia* give lower values; these will weight the lower end of the frequency histogram according to the relative proportion of spores in equatorial aspect on a slide, but since this proportion and any distinct size differences of the maximum diameter in equatorial view depend on the structure of the spore it will enhance the diagnostic value of the histogram.

Variability is expected and is much more easily observed in a thick exine such as that of *Pelletieria* than in a thin one, and for this reason the ranges of the minor *Ruffordia* measurements have not been given. Similarly a dimensionless coefficient of variation has been calculated (ratio: standard deviation/mean maximum diameter, expressed as a percentage) for the distributions of maximum diameters, to make clearer comparison between species.

We accept an estimated observation error of $2\frac{1}{2}$ per cent for reasonable speed of working, and thus validly submerge human partiality for round numbers in a five point moving average (text-fig. 7A, B).

The span of four muri should be measured in a distal inter-radial area, and the shape of muri in optical sections where the plane containing the murus is perpendicular to the slide. Exine thickness should be measured inter-radially.

It is likely that spore 'populations' of varying preservational states, extracted from diagenetically different rock samples may give different measurements; maceration treatment may also cause differences. In these cases the difference from the holotype and type-range (from the type locality) will be systematic and open to experimental investigation and rationalization. Knowledge of these differences will widen the scope of the taxon description, contributing information about the chemical and physical behaviour of exines in different species. Similarly it will make specimens which are other than 'well preserved' more precisely identifiable for stratigraphical use.

PURPOSE OF THIS STUDY

It is hoped that the straightforward presentation of measurements and of plots of possible linear proportionality between pairs of characters for a large number of specimens of these *in situ* spores may provide sufficient ground for confidence in subsequent erection of stratigraphically useful dispersed spore species of *Cicatricosisporites* s.l. in the Early Cretaceous. Extreme 'lumping' by Couper (1958) and others into the irrelevant Eocene species *C. dorogensis*, and very imperfect original typification of that and of many other dispersed spore species still being erected has led to a situation in which virtually no stratigraphic use can now be made of spores of this type within the Lower Cretaceous. With the small number of characters available successive species will clearly overlap in morphography, but if a species is typified from one precise source or sample with analysis of variation given on an adequate number of specimens it is hoped that some further progress will be possible.

As it is clear that few characters can be observed in all (or even most) of the specimens, an overall number of 200 is considered necessary for *in situ* spores, and 100 specimens is a minimum for dispersed spores even when comparable observations for *in situ* spores are available.

THE DISPERSED SPORE GENUS *ICATRICOSISPORITES*

Range. Dettmann (1963, p. 74) has shown that *Contignisporites* may be separated in morphography and in possible affinities from *Cicatricosisporites*. As *Corrugatisporites* (Early Jurassic) may also be easily distinguished, it is not necessary to extend the range of *Cicatricosisporites* down through the Jurassic as is done by Kedves and Sole de Porta (1963) and others; the true range begins in the latest Jurassic (at about the top Kimmeridge Clay of England), and the spores are only at all common from the earliest Cretaceous onwards.

Comparison. We believe that in the earliest Cretaceous there is no distinct genus *Plicatella*, although by Barremian and Aptian times radial equatorial exine thickening may well be diagnostic of distinct taxa. Study of *Pelletieria* has shown that occasional thickenings occur in radial and proximal regions but that they are within the species 'population'. As none of the earliest Cretaceous records of *Plicatella* (*Appendicisporites tricornitatus* etc.) are supported by more than a very few specimens (Couper 1958, Lantz 1958a, Hughes 1958), there is not yet any contrary evidence; the material of Lantz 1958b, Pocock 1962, Brenner 1963, Singh 1964 is probably of Barremian or later age.

The establishment of a definite range beginning for *Plicatella*, and its separation from the later *Appendicisporites*, must await the erection of properly based species, as indicated above.

The separation of such spores from *Cicatricosisporites* appears to be a more complex matter than measurement of the thickness of part of the wall (Pocock 1964, p. 162), apart from the difficulty that the 'wall layers' do not appear in our sections (Pl. 44, 45) which thus fail to support the diagrams of Pocock (1962, p. 162, figs. 16, 17).

Use of the genus. We reject as undesirable and unworkable the proposal of Pocock (1964, p. 156) to use *Cicatricosisporities* 'as an organ genus of the (extant) genus *Molria* and morphologically related fossil species'. We believe that it should remain as a form genus at least until the Cretaceous and Tertiary history of the plant groups involved has been worked out with macrofossils or until the diagnoses of the extant genera (*Molria* etc.) have been properly emended to include the fossils, as suggested by Hughes (1963).

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VARIATION AND ONTOGENY OF SOME OXFORDIAN AMMONITES: *TARAMELLICERAS* *RICHEI* (DE LORIO) AND *CRENICERAS* *RENGGERI* (OPPEL), FROM WOODHAM, BUCKINGHAMSHIRE

by D. F. B. PALFRAMAN

ABSTRACT. Statistical and ontogenetic studies of *Taramelliceras richiei* (de Loriol) and *Creniceras renggeri* (Oppel) have shown identity in their early stages. Variation in protoconch size is consistent and small, as is the diameter of the nepionic constriction. Divergence in shell form occurs only at the onset of maturity, which in *C. renggeri* begins at about 8.4 mm. and in *T. richiei* at about 18.8 mm. It is concluded that the two 'species' are a sexually dimorphic pair. The name *C. renggeri* has priority.

A COLLECTION of Lower Oxfordian ammonites was made from the Woodham Brick Company's Pit, with the objective of studying the variation and ontogeny of selected species. The pit is situated almost midway between Bicester and Aylesbury, near Ake-man Street Station, Buckinghamshire (Grid. Ref. 707186), and exposes some seventy feet of Oxford Clay (Arkell 1939). A lithological unit 'The Lamberti Limestone', a bed one foot thick, separates the lowermost forty feet of clay (Athleta Zone) from the uppermost thirty feet (Mariae Zone).

The Mariae Clays, as the beds of the Mariae Zone are here named, furnished the material studied. Both 'species' examined in this paper occur, together, throughout the Mariae Clays at Woodham; they are commonest in the lower ten feet of the Mariae Zone (generally pyritized), becoming rare in the upper twenty feet of beds (generally limonitized). They are both found together at all levels at Woodham. There is no evidence to suggest that either *Taramelliceras richiei* (de Loriol) or *Creniceras renggeri* (Oppel) occurs outside the Mariae Zone in this country. However, both species appear to have arisen in the Upper Lamberti Zone, being found in Haute-Saône (Maire 1908). They are both found together in the Renggeri Marls (Mariae and Cordatum Zones) of the Jura Mountains, where they are fairly common (de Loriol 1898-9, 1900 and Arkell 1939). As far as the author is aware they are not recorded above the Cordatum Zone; though, as Arkell (1939) says '... exact details of range [are] usually not available'.

All the specimens collected are preserved as internal moulds, pyritic near the base of the zone becoming limonitic towards the top. No original shell material has been found among the collection of several thousand ammonites. In a few individuals the innermost whorls are calcified, but rarely to a diameter of more than 3-4 mm. Some, which are otherwise completely pyritized or limonitized, were found to have a calcareous protoconch.

Very few specimens were found preserved as pyrite or limonite moulds above a maximum diameter of 2 or 3 cm. and it seems that there is a maximum size above which ammonites were not pyritized or limonitized. Internal moulds composed of clay, seen *in*

situ, showed that some ammonites must have had a diameter of not less than forty centimetres (see Pl. 48, fig. 1); often in the centre of such moulds were to be seen pyritized or limonitized nuclei of familiar dimensions.

Nearly five hundred specimens of *Taramelliceras richei* (de Loriol) and over two hundred specimens of *Creniceras renggeri* (Oppel) have been examined in this work. All specimens collected by, or given to, the author are in the University Museum, Oxford and are prefixed by OUM, those borrowed from the British Museum (Natural History) by BM. The following abbreviations are also used throughout the text: D = diameter, W = whorl width, HH = whorl height, U = umbilical diameter.

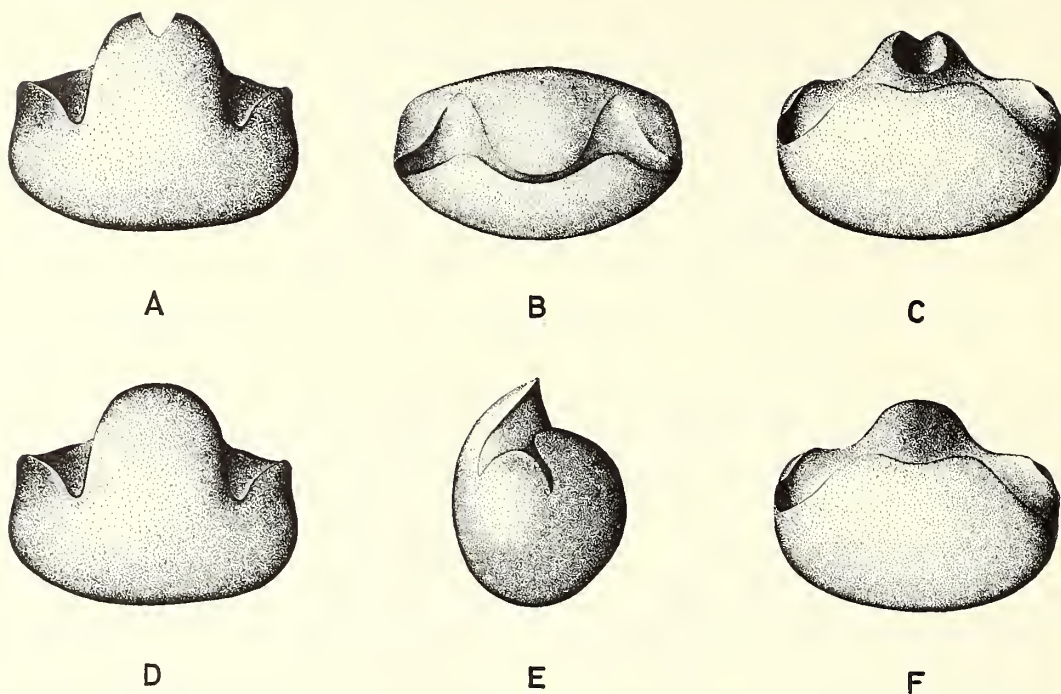
VARIATION AND ONTOGENY OF *TARAMELLICERAS RICHEI* (DE LORIOL)

Due to the conditions of preservation, the most frequently occurring form in which *Taramelliceras richei* (de Loriol) was found at Woodham, was as internal moulds of the phragmocone. The type material of *T. richei* is based largely on internal moulds of phragmocones (de Loriol 1898). In the author's collection of nearly five hundred specimens less than 10 per cent. have any part of the body chamber preserved, and in none of these is it complete. The species is a typical oppelid, being compressed and involute with a small umbilicus. Whorl height is approximately half the diameter, whorl width is approximately quarter the diameter. Coiling is regular in the phragmocone, but on the body chamber of adults the umbilical seam begins to uncoil.

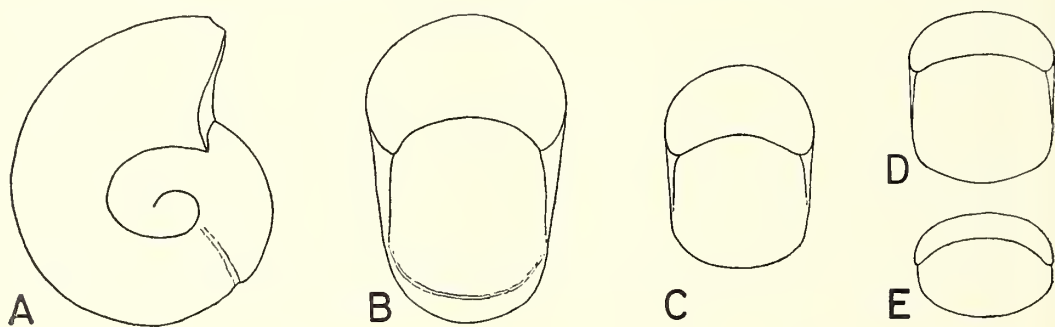
Protoconch. Less than 5 per cent. of the specimens of *T. richei* available were found to have protoconchs preserved; in all some eight protoconchs were dissected out. These are beautifully preserved as smooth pyritic moulds, showing details of the prosuture (text-fig. 1 and Pl. 48, fig. 4). In all cases the protoconchs are barrel-shaped with a width greater than the diameter. The largest recorded diameter of a protoconch of *T. richei* is 0.30 mm., the smallest 0.25 mm. (see Table 1). In one specimen (OUM J25230) the caecal mould is visible (text-fig. 1A, C).

Phragmocone. Just as the surface of the protoconch internal mould is smooth, so also is the first whorl of growth. The nepionic constriction occurs after one complete whorl of growth from the prosepium, at a diameter of about 0.53 mm., or roughly twice that of the protoconch (Table 1).

The nepionic constriction is well-defined, especially in the ventral and ventro-lateral regions, fading on the flanks and almost imperceptible near the umbilicus (text-fig. 2A, B; Pl. 48, fig. 6). In *T. richei* there is no ornamental difference, on the internal mould, between the whorl preceding the nepionic constriction and that immediately succeeding. In some ammonites, *Kosmoceras* and *Garantiana*, Makowski (1962) noted that the ornamentation characteristics of the full-grown shell appeared after the nepionic constriction. Ontogenetic features of note are: a decrease in the W/D ratio from the protoconch to a diameter of 0.8–1.0 mm. and a similar decrease in the U/D ratio to about the same diameter. From a diameter of 0.8–1.0 mm. onwards, growth is almost isometric until the onset of maturity which occurs at a diameter of about 18–20 mm. This is graphically represented here (text-figs. 3 and 4). From a diameter of 0.8–1.0 mm. until the onset of maturity the HH/D ratio shows almost isometric growth (text-fig. 5).



TEXT-FIG. 1. Protoconchs of *Taramelliceras richei* (de Loriol); Mariae Zone, Woodham, Bucks., England. A and D, ventral view; B, inclined apertural view; C and F, apertural view; E, side view. A and C based on OUM J25230; B, D, E, and F based on OUM J25228. All $\times 100$.



TEXT-FIG. 2. Diagram of the innermost whorls of *Taramelliceras richei* (de Loriol); Mariae Zone, Woodham, Bucks., England. A and B, showing the position of the nepionic constriction; E, protoconch. A, B, C, and D, drawn from OUM J25038; E, drawn from OUM J25234. All $\times 50$.

Ribbing is completely absent until a diameter of about 4 mm.; at this diameter radial umbilical swellings begin, strongly near the umbilicus but fading on the flanks. The ribs are shallow and distant and are initially eight to ten per whorl. It is not until a diameter of about 8–10 mm. that ribbing is differentiated into primaries and intercalatories (Pl. 50, fig. 1a, c).

TABLE 1. Measurements in millimetres of the dimensions of protoconchs and the diameter of the nepionic constriction in specimens of *Taramelliceras richei* (de Loriol). All specimens from University Museum, Oxford (OUM). All specimens from the Mariae Zone, Woodham.

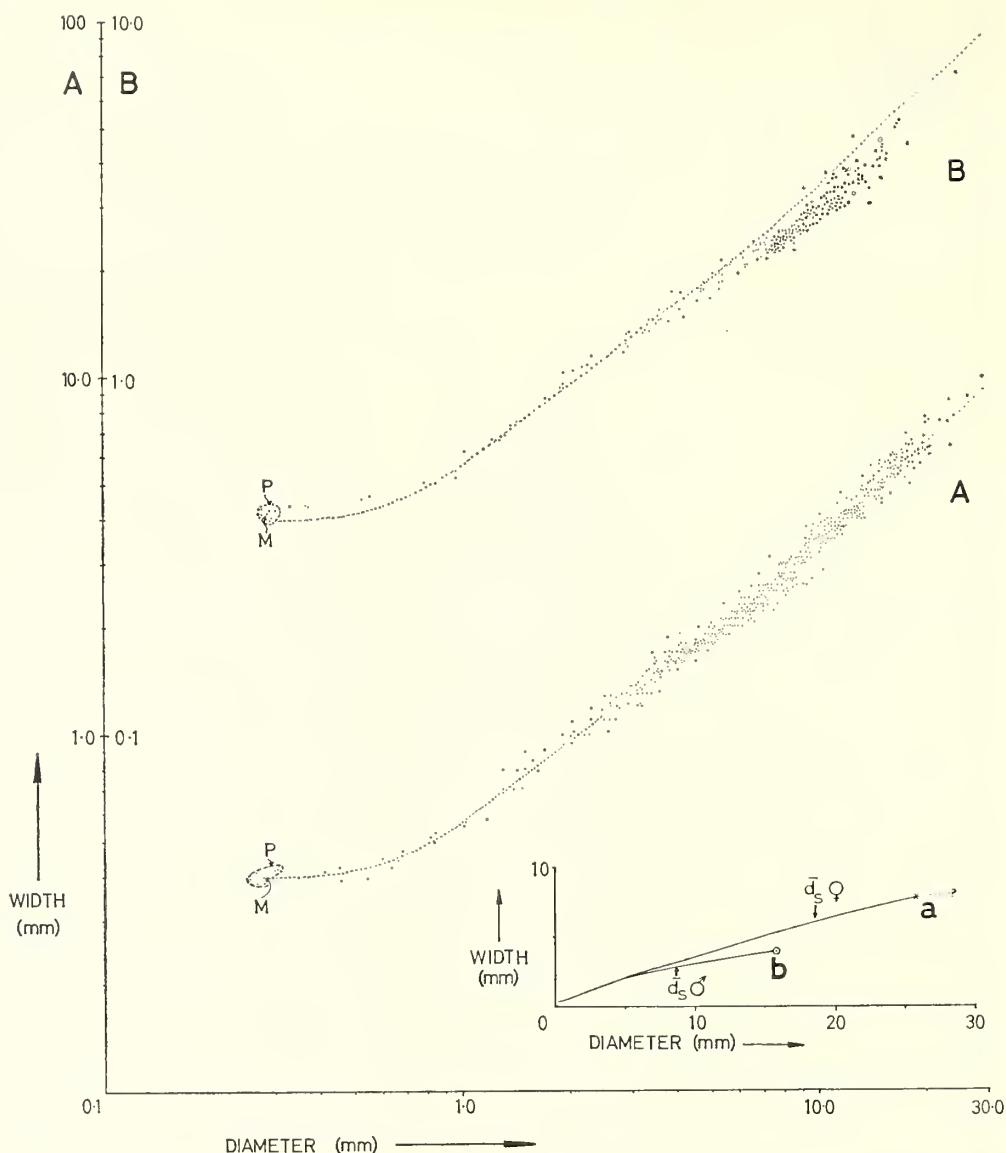
Specimen Number	Protoconch		Nepionic Constriction
	D	W	D
J25024			0.53
J25038			0.54
J25040	0.28	0.40	0.54
J25042			0.54
J25045	0.27	0.38	
J25046	0.25	0.40	0.56
J25228	0.30	0.42	0.53
J25230	0.30	0.42	0.53
J25231	0.28	0.41	0.52
J25232	0.27	0.41	0.52
J25234	0.28	0.38	0.53

Differentiated ribbing is undoubtedly a characteristic of *T. richei*, all specimens showing this feature to some degree, with a variation from relatively coarse ribbing to fine (Pl. 49, figs. 1*a*, *b*, 2*a*, *c*). On the final whorl of all adult specimens there are two series of ribs; primaries and intercalatories. The primary ribs generally number ten to twelve per whorl, developing initially as radial umbilical swellings then fading on the flanks and finally becoming relatively sharp and distinct on the ventro-lateral area. They are slightly sinuous with marked ventro-lateral prorsiradiation (Pl. 48, fig. 2*a*; Pl. 49, figs. 1*a*, 2*a*, 4*a*; Pl. 50, fig. 1*a*). Ribs always fade on the venter of internal moulds, but may not do so on the actual surface of the shell. In some cases the venter is smooth (see Pl. 49, fig. 1*b*), whereas in most instances the ribbing simply becomes weaker in the ventral region (Pl. 49, fig. 2*b*). On the last quarter of the adult phragmocone whorl, nearly all specimens develop feeble ventral tubercles, which become stronger adorally (Pl. 49, fig. 4*a*, *b*; Pl. 50, fig. 1*a*, *b*). The tubercles coincide at the point at which opposing ribs, on either side of the venter, both primaries and intercalatories, would meet had they continued uninterrupted across the venter.

The intercalatory ribs, on the final whorl of adult specimens, generally number about forty. They are restricted to the ventro-lateral area and are identical in form with the primary ribs in this region, by way of amplitude, sharpness and direction, for each particular specimen. Between each primary rib are three to four intercalatories (Pl. 48, fig. 2*a*; Pl. 49, figs. 2*a*, 4*a*; Pl. 50, fig. 1*a*).

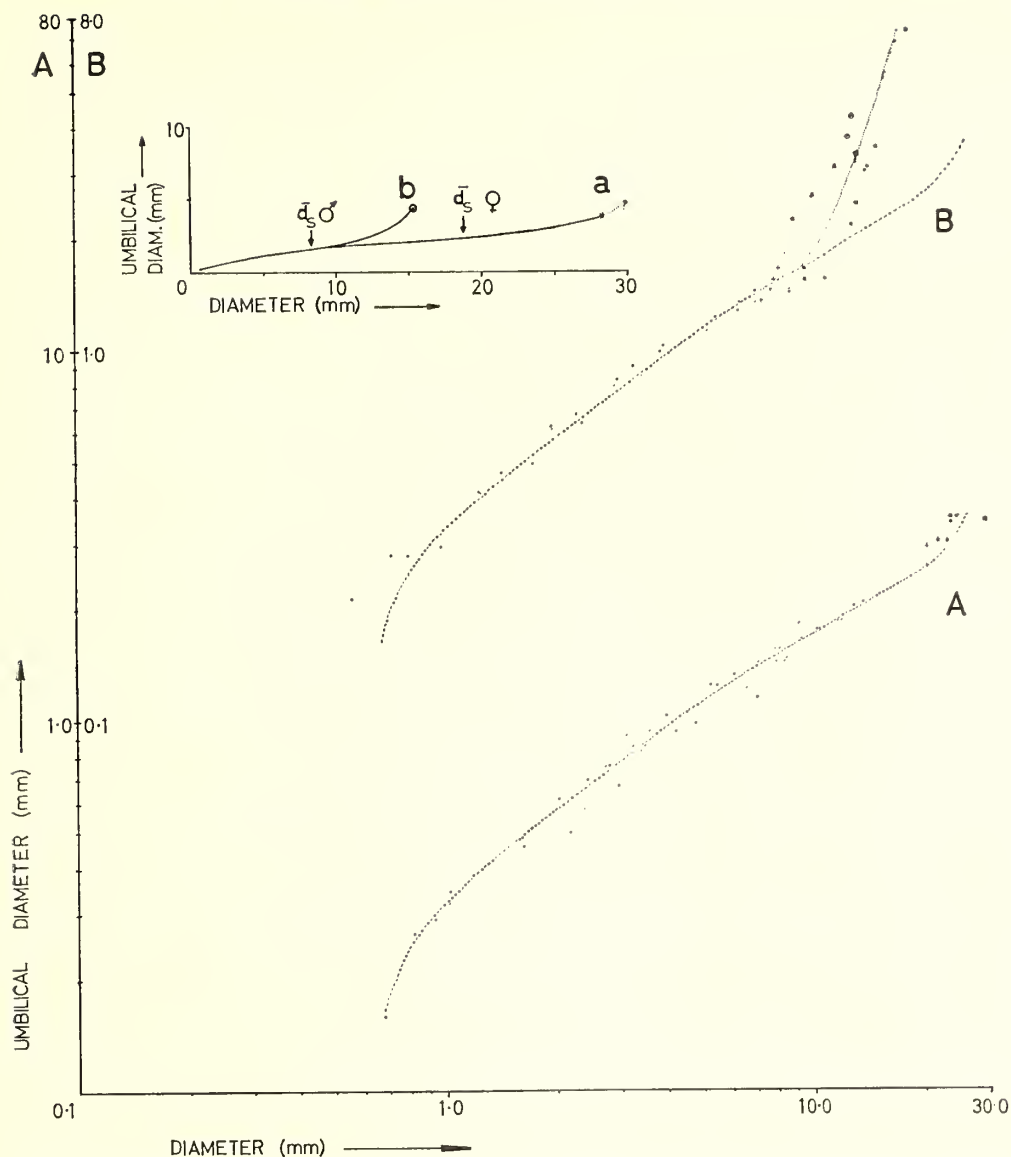
The mean maximum diameter of the phragmocone, of more than two hundred adult specimens, was found to be 18.8 mm., with a standard deviation (σ) of 1.51. The coefficient of variation ($V = 100\sigma/m$, where m is the mean maximum diameter, $\bar{d}_s$, of the adult phragmocones) is 8.02. The greatest diameter at which the septa are approximated was found to be 27 mm., the smallest 14 mm. (text-fig. 6). The phragmocone generally comprised $6\frac{1}{4}$ –7 whorls from the prosepium. Variation in the whorl-shape is here shown diagrammatically (text-fig. 7 and Pl. 48, fig. 2*a*).

The sutural ontogeny of *T. richei* develops in a way which, in Jurassic ammonites, is beginning to appear fundamental (Schindewolf 1954). The prosuture is significantly



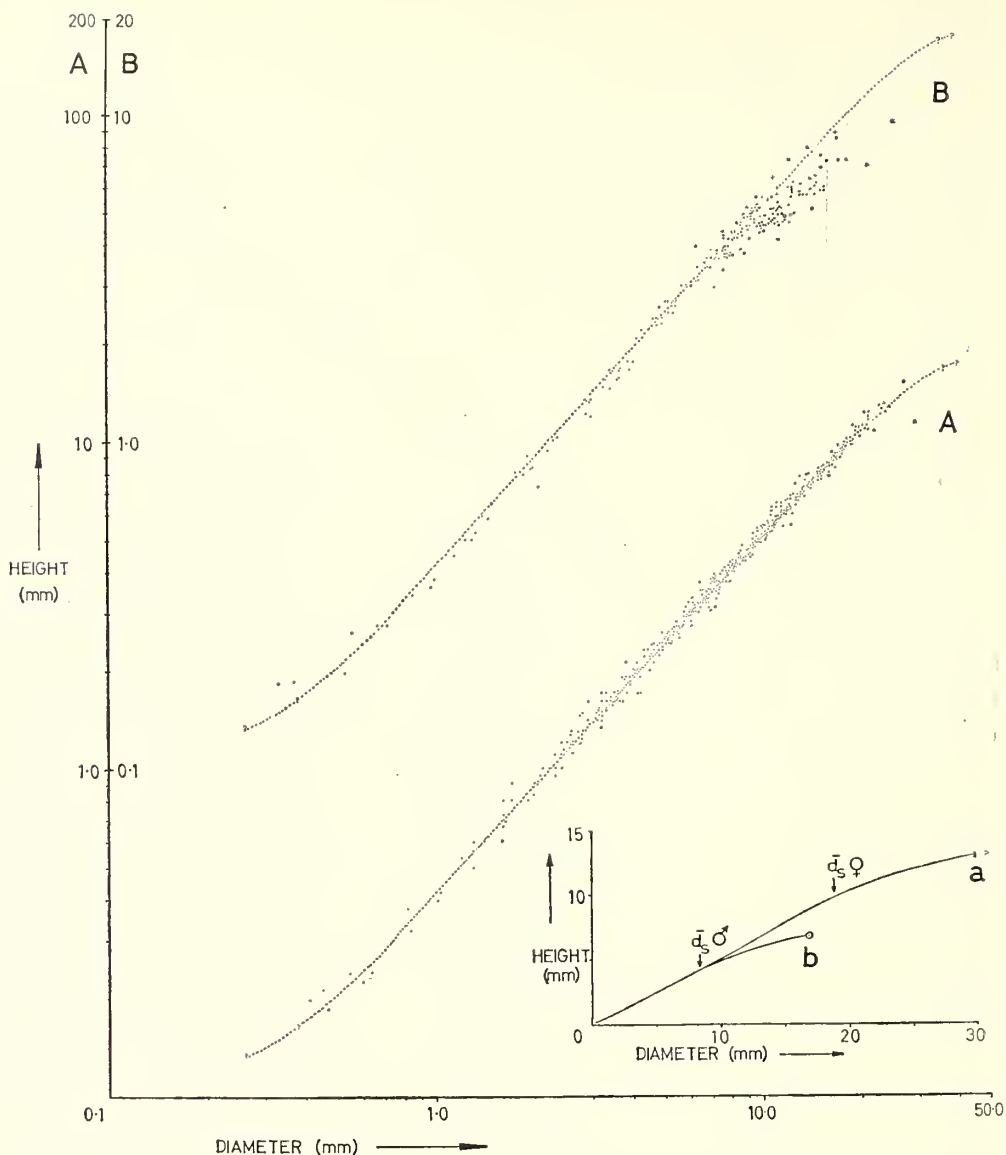
TEXT-FIG. 3. Graphs showing the relationship between diameter and whorl width of *Taramelliceras richiei* (de Loriol), and of *Creniceras renggeri* (Oppel). The two graphs are superimposed: the diameter axis is common, the width axis is divided into A and B scales, the B scale being one log cycle behind the A scale. Graph A (W/D for *T. richiei*) is controlled by the A scale, graph B (W/D for *C. renggeri*) is controlled by the B scale. The fine dashed line on graph B is that superimposed from graph A (approximate best-fit line). The areas denoted by P (coarse dashed line) enclose measurements made on the protoconchs: M is the mean of these measurements. Encircled dots represent measurements made at the maximum diameter of complete adults: asterisks—measurements made on adult body-chambers: crosses—measurements made at the adoral end of adult phragmocones: dots—measurements made on immature phragmocones.

Inset. The same graphs plotted on a linear scale and having both axes common. a, W/D for *T. richiei*; b, W/D for *C. renggeri*. The arrowed points, $\bar{d}_s \text{ ♀}$ and $\bar{d}_s \text{ ♂}$, mark the position of the mean septate diameter of mature specimens of supposed female and male respectively. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 4. Graphs showing the relationship between diameter and umbilical diameter of *Taramelliceras richiei* (de Loriol), and of *Creniceras renggeri* (Oppel). The two graphs are superimposed: the diameter axis is common, the umbilical diameter axis is divided into A and B scales, the B scale being one log cycle behind the A scale. Graph A (U/D for *T. richiei*) is controlled by the A scale, graph B (U/D for *C. renggeri*) is controlled by the B scale. The fine dashed line on graph B is that superimposed from graph A (approximate best-fit line). Conventions as for text-fig. 3.

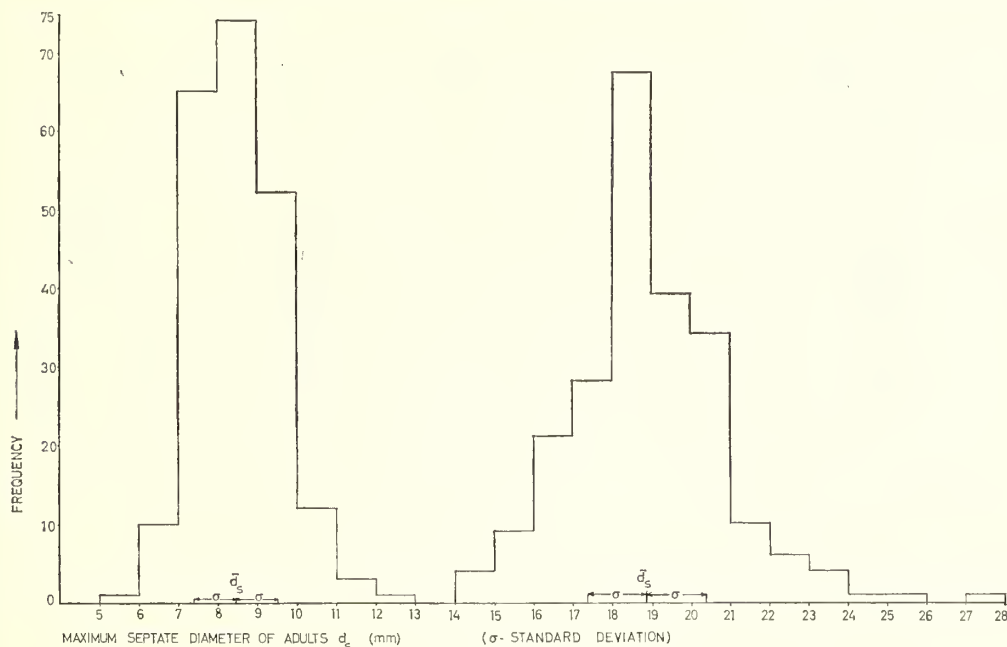
Inset. The same graphs plotted on a linear scale and having both axes common. *a*, U/D for *T. richiei*; *b*, U/D for *C. renggeri*. The arrowed points, $\bar{d}_s \text{ } \bar{\text{f}}$ and $\bar{d}_s \text{ } \bar{\text{m}}$, mark the position of the mean septate diameter of mature specimens of supposed female and male respectively. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 5. Graphs showing the relationship between diameter and whorl height of *Taramelliceras richi* (de Loriol), and of *Creniceras renggeri* (Oppel). The two graphs are superimposed: the diameter axis is common, the height axis is divided into A and B scales, the B scale being one log cycle behind the A scale. Graph A (HH/D for *T. richi*) is controlled by the A scale, graph B (HH/D for *C. renggeri*) is controlled by the B scale. The fine dashed line on graph B is that superimposed from graph A (approximate best-fit line). Conventions as for text-fig. 3.

Inset. The same graphs plotted on a linear scale and having both axes common. *a*, HH/D for *T. richi*; *b*, HH/D for *C. renggeri*. The arrowed points, $\bar{d}_s \text{♀}$ and $\bar{d}_s \text{♂}$, mark the position of the mean septate diameter of mature specimens of supposed female and male respectively. All specimens from the Mariae Zone, Woodham.

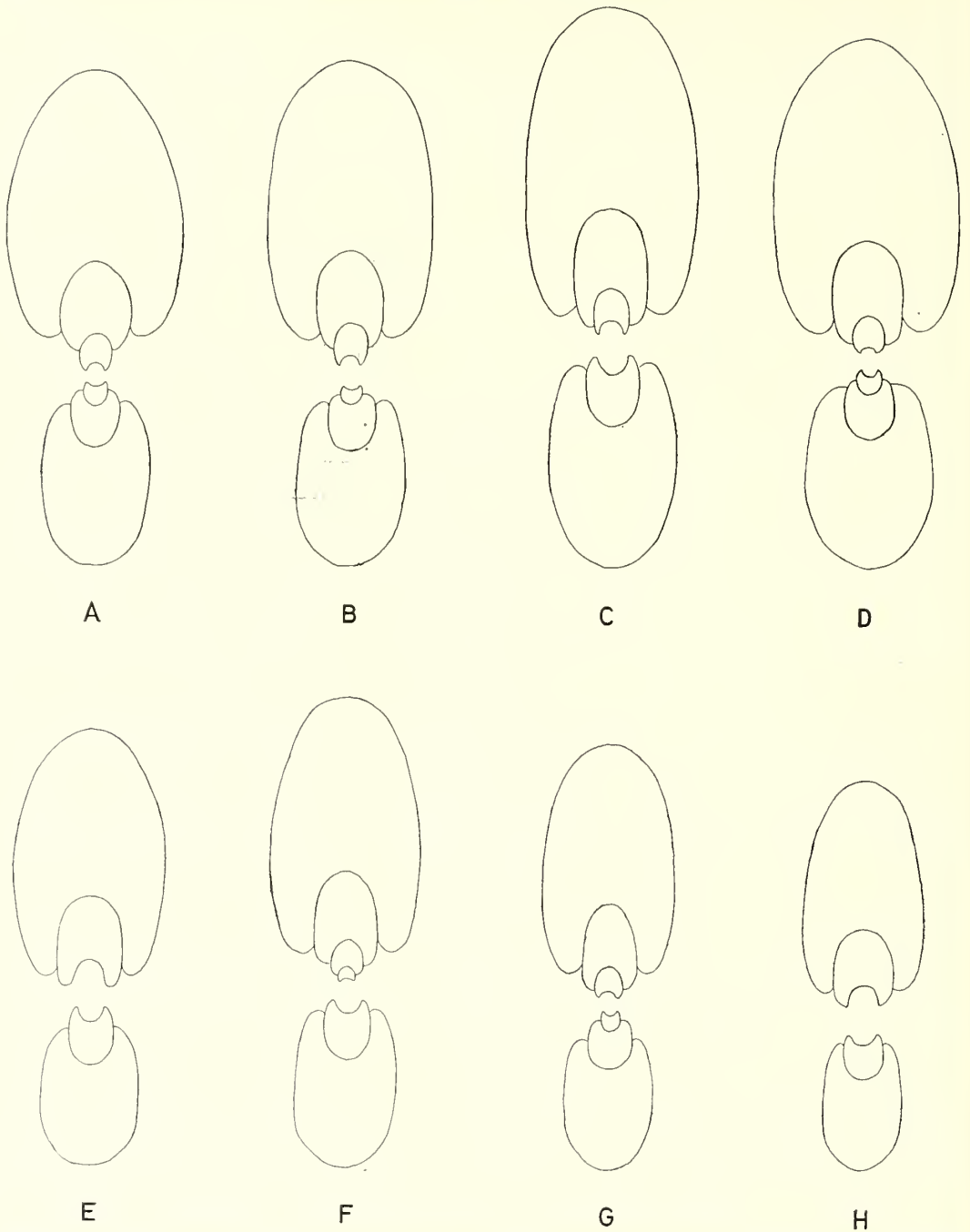
different from the primary suture, having a very large ventral saddle. The primary suture (text-figs. 1 and 8) is divided into: external (or ventral), lateral, U_2 , U_1 , and dorsal lobes, with corresponding saddles between. These first-formed lobes have been called 'protolobes' by Schindewolf (1954): subsequent works (Schindewolf 1960, 1962, and 1963) have shown that these basic protolobes are common to all Jurassic ammonites so far investigated. Addition of successive sutural elements in *T. richei* occurs at the



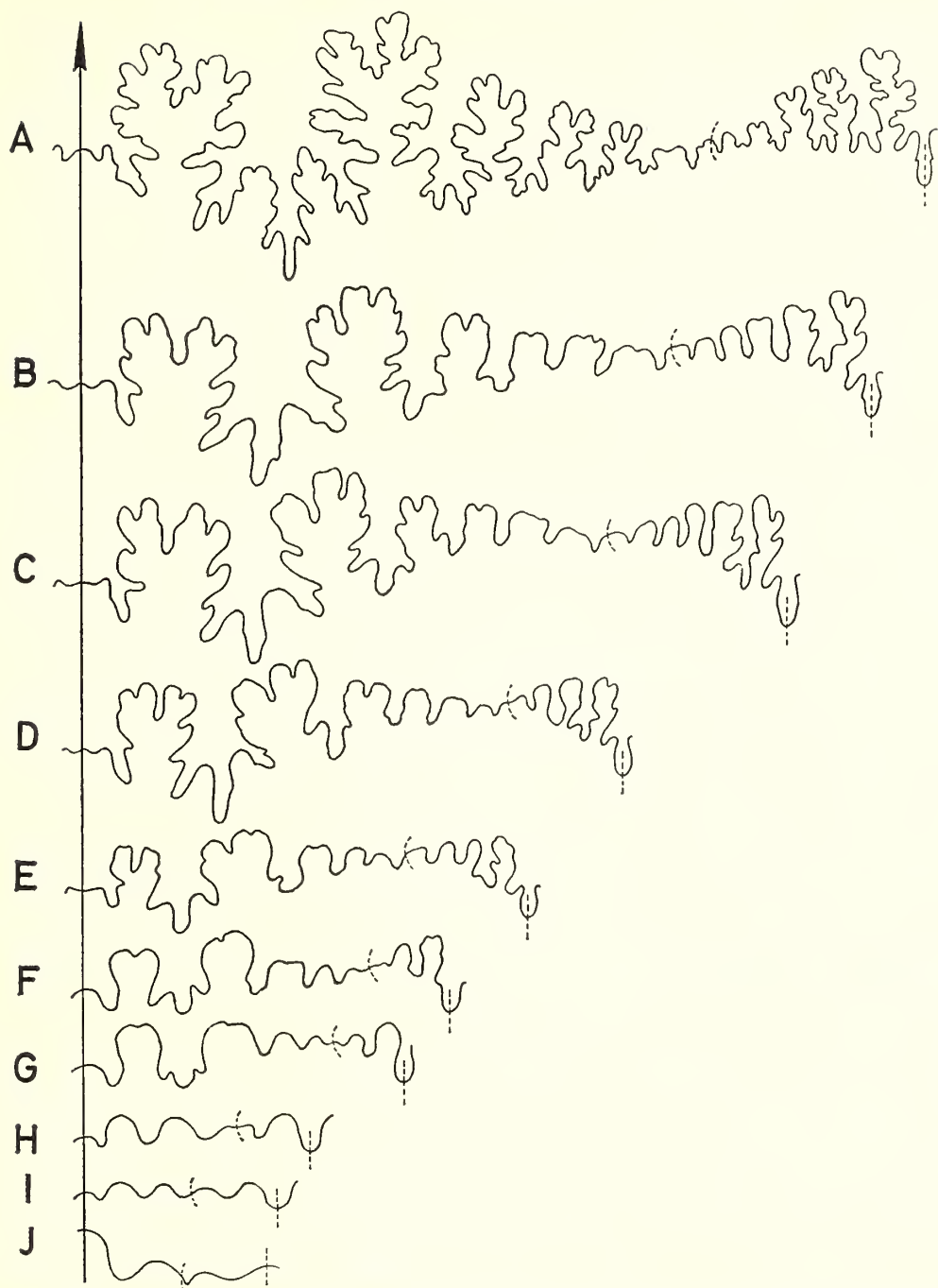
TEXT-FIG. 6. Histogram showing the variation in the diameter at which septation ceases (d_s) in mature specimens of *Taramelliceras richei* (de Loriol) and in *Creniceras renggeri* (Oppel). The *T. richei* range is from 14–28 mm., the *C. renggeri* range from 5–13 mm. All specimens from the Mariae Zone, Woodham.

umbilical seam; this is the 'U-type' ontogeny of Schindewolf (1954). The final sutures of adult specimens are greatly differentiated into several complex saddles and lobes (text-fig. 8A). Sutural approximation, generally regarded as a feature of maturity, is commonly to be seen in most specimens with a phragmocone diameter of 18–19 mm. (Pl. 48, fig. 2a; Pl. 49, figs. 2a, 4a, 4b; Pl. 50, fig. 1a).

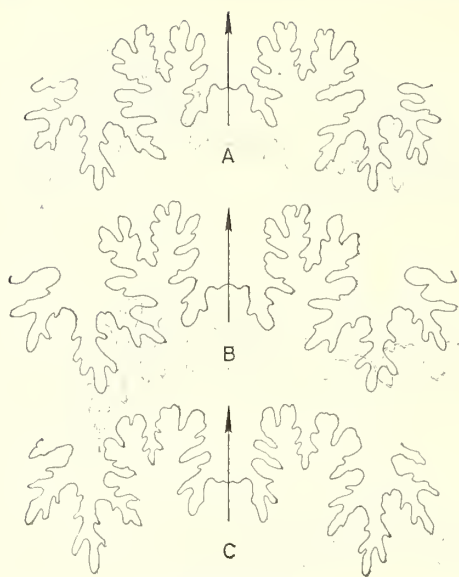
In the adult sutures the largest saddles are the first and second lateral and the largest lobes the ventral and lateral. These major sutural elements show the greatest range of variation and have been compared on either side of the venter in the same specimen, and on the same side of the venter at similar diameters, in different specimens. Comparing the same sutural elements, on either side of the venter for any single specimen, shows remarkably little variation (text-fig. 9). The greatest difference recorded is in the frilling of the most adapical accessory lobe: even so this difference is somewhat subtle and does not compare with the wide intraspecific sutural variation shown by *Morrisiceras morrisi* (Oppel) and *Clydoniceras discus* (Sow.) mentioned by Arkell (1957).



TEXT-FIG. 7. Cross-sections through the phragmocone of *Taramelliceras richei* (de Loriol). A, OUM J25041; B, OUM J25021; C, OUM J25010; D, OUM J25239; E, OUM J25241; F, OUM J25236; G, OUM J25005; H, OUM J25238. All $\times 4$. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 8. Sutural ontogeny of *Taramelliceras richei* (de Loriol). A, OUM J25013, $\times 9$ ($D = 15$ mm.); B, OUM J25036, $\times 15$ ($D = 8.7$ mm.); C, OUM J25036, $\times 18$ ($D = 6.4$ mm.); D, OUM J25036, $\times 20$ ($D = 4.6$ mm.); E, OUM J25036, $\times 25$ ($D = 3.13$ mm.); F, OUM J25036, $\times 30$ ($D = 2.13$ mm.); G, OUM J25036, $\times 35$ ($D = 1.53$ mm.); H, OUM J25036, $\times 50$ ($D = 0.85$ mm.); I, OUM J25040, $\times 50$ ($D = 0.32$ mm.); J, OUM J25040, $\times 50$ ($D = 0.28$ mm.). I, primary suture. J, prosuture. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 9.



TEXT-FIG. 10.

TEXT-FIG. 9. Sutural variation in *Taramelliceras richei* (de Loriol). A, OUM J25230 ($D = 12.2$ mm.); B, OUM J25228 ($D = 12.0$ mm.); C, OUM J25229 ($D = 12.1$ mm.). All $\times 7.5$. All specimens from the Mariae Zone, Woodham.

TEXT-FIG. 10. Sutural variation in *Taramelliceras richei* (de Loriol). A, OUM J25029 ($D = 12$ mm.); B, OUM J25028 ($D = 12.4$ mm.); C, OUM J25009 ($D = 11.8$ mm.); D, OUM J25035 ($D = 12$ mm.); E, OUM J25024 ($D = 12$ mm.); F, OUM J25026 ($D = 12$ mm.). All $\times 7.5$. All specimens from the Mariae Zone, Woodham.

Variation between the same sutural elements of different specimens, at approximately the same diameter, shows relatively marked differences (text-fig. 10). These differences are generally of size, however, the disposition of the elements being essentially the same. The most marked differences are between the specimens OUM J25029 and OUM

EXPLANATION OF PLATE 48

Fig. 1. Internal clay mould of a large *Peltoceras*(?) sp.; basal Mariae Zone (about 5 ft. above the Lamberti Limestone), Woodham, Bucks. $\times \frac{1}{10}$.

Fig. 2. *Taramelliceras richei* (de Loriol, OUM J25571. Adult phragmocone. a, side view; b, apertural view. Both $\times 3$.

Fig. 3. *T. richei*, BM C. 39588; Oxford Clay, Scarborough, Yorkshire. $\times 1$.

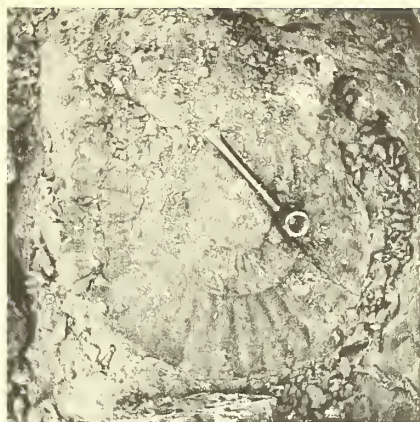
Fig. 4. *T. richei*, OUM J25234 (lost); Mariae Zone, Woodham, Bucks. Protoconch. $\times 50$.

Fig. 5. *T. richei*, OUM J25672. Adult specimen. a, side view; b, ventral view. The body-chamber occupies about $\frac{1}{3}$ of the final whorl. Both $\times 3$.

Fig. 6. *T. richei*, OUM J25038. Innermost whorls showing the nepionic constriction. $\times 40$.

Fig. 7. *T. richei*, BM 39642; Oxford Clay, Scarborough, Yorkshire. Stereopair of adult specimen showing the nature of the peristome and ventro-lateral spines. $\times 1$.

Fig. 1—unwhitened; Figs. 2a, b, 3, 5a, b, and 7—whitened with ammonium chloride; Figs. 4 and 6—whitened with magnesium oxide. All specimens from the Mariae Zone, Woodham, Bucks., unless otherwise stated.



1



2a



2b



3



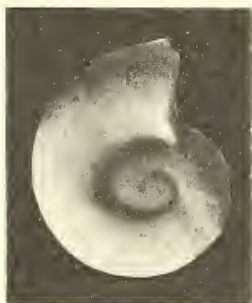
5a



5b



4



6



7



J25024 (text-fig. 10A, E). Generally speaking it seems fairly safe to say that the intra-specific sutural variation in *T. richei* is extremely small.

Body-chamber. The body-chamber of adult specimens of *T. richei* is quite different from the phragmocone. The most marked change is in the development of ventral and ventro-lateral spines. In some specimens spines develop quite suddenly after the last septum in both positions. Specimen OUM J25676 shows the ventral spines beginning first, the ventro-lateral spines developing later (Pl. 49, fig. 3a, b). The ventro-lateral spines are paired and alternate with those on the venter, relative to the median plane. Not all body-chambers, of specimens which are otherwise identical, become spinose: they merely retain the ventral tubercles of the adult phragmocone (Pl. 48, fig. 5a, b). However, there is probably a whole range between tuberculate venters only, and spinose venters and ventro-lateral regions: this is supported by a collection of specimens from the Oxford Clay of Warboys, Hunts. (BM C.4333, C.10651, C.15960, C.16009, C.16010, C.19286, and C.19296), which shows precisely this range.

Ribbing on the body-chamber appears to be weaker than on the phragmocone, but the very poor preservation of the body-chambers of Woodham specimens may affect this feature. Some of the better preserved specimens from Warboys show well-defined ribs, both primaries and intercalatories, even on the flanks of the body-chamber (BM C.4333 and C.15960). The phragmocones of these specimens are otherwise identical with those from Woodham.

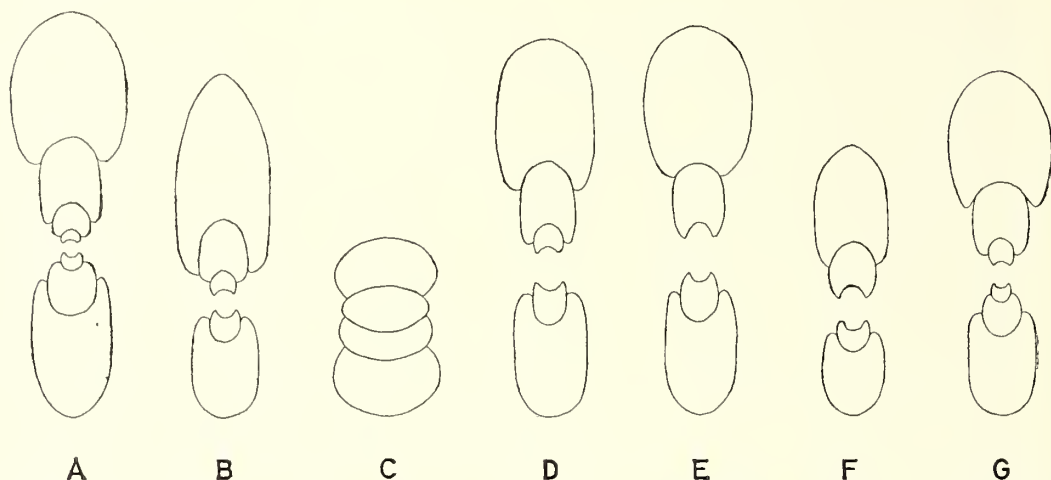
As would be expected in the final stages of adult specimens, the body-chamber uncoils at the umbilical seam (Pl. 49, fig. 3b and text-fig. 4). Among the Woodham specimens the author was unable to find an adult which showed the nature of the peristome. However, among three specimens from the Oxford Clay of Scarborough, Yorkshire (BM 39642, C.39588, and C.39589), labelled *Proscaphites oculatus* (Phillips), is one specimen (BM 39642) which shows the nature of the peristome (Pl. 48, fig. 7). These specimens are almost certainly conspecific with *T. richei*, developing ventral and ventro-lateral spines (Pl. 48, figs. 3 and 7): unfortunately the phragmocone is not preserved and the body-chamber of the specimens is crushed. The peristome of BM 39642 is fairly simple, its outline coinciding with the course of the primary ribs. The diameter of the almost complete specimen (45 mm.), which has a body-chamber of three-quarters of a whorl, is in agreement with the predicted size of complete adults from Woodham, assuming that the Woodham specimens have a body-chamber of about three-quarters of a whorl. If this is so, the total number of whorls from the proseptum is from $7-7\frac{3}{4}$ in *T. richei*.

Among the better preserved specimens from Woodham, the phragmocone is a dull black colour, whereas that of the body-chamber is a golden reflective (if pyritic) mould. The dull black colour extends just on to the body-chamber, and in many cases a well-defined line can be traced between the black and golden parts of the body-chamber. The line is almost co-incidental with the course of the primary ribs but with slightly greater ventral prorsiradiation. This line may represent the annulus (Crick 1898): however, no muscle-scars were recorded from any specimen of *T. richei* from Woodham.

VARIATION AND ONTOGENY OF *CRENICERAS RENGGERI* (OPPEL)

Creniceras renggeri is a smaller 'species' than *Taramelliceras richei*, complete adults rarely attaining a diameter of more than 20 mm. It appears that because of its small

size *C. renggeri* is generally to be found complete, or nearly so, as it rarely exceeds the optimum size for complete preservation as a pyritic or limonitic mould in the Oxford Clay of Woodham.



TEXT-FIG. 11. Cross-sections through *Creniceras renggeri* (Oppel) A, OUM J25294; B, OUM J25378; C, OUM J25378 (inner whorls of B); D, OUM J25298; E, OUM J25305; F, OUM J25322; G, OUM J25272. All except fig. C are $\times 4$; fig. C $\times 30$. All specimens from the Mariae Zone, Woodham.

TABLE 2. Measurements in millimetres of the dimensions of protoconchs and the diameter of the nepionic constriction in specimens of *Creniceras renggeri* (Oppel). All specimens from the University Museum, Oxford (OUM). All specimens from the Mariae Zone, Woodham.

Specimen Number	Protoconch		Nepionic Constriction D
	D	W	
J25305	0.29	0.40	
J25308	0.30	0.42	
J25347	0.29	0.42	
J25364	0.28	0.41	0.54
J25368	0.28	0.42	0.53
J25378	0.29	0.41	0.56

Protoconch. Ontogenetically *C. renggeri* goes through identical stages as *T. richei* until the onset of maturity. Protoconchs are identical in shape to, and vary within almost the same limits as, those of *T. richei* (Table 2, cf. Table 1).

EXPLANATION OF PLATE 49

Taramelliceras richei (de Loriol). All specimens are from the Mariae Zone of Woodham, Bucks. and have been whitened with ammonium chloride. All $\times 3$.

Fig. 1. OUM J25482. Adult phragmocone. *a*, side view; *b*, ventral view. Fig. 2. OUM J25617. Adult phragmocone. *a*, side view; *b*, ventral view. Fig. 3. OUM J25676. Adult specimen; the body-chamber occupies the last half-whorl; ventral and ventro-lateral spines are developed. *a*, ventral view; *b*, side view. Fig. 4. OUM J25455. Adult phragmocone. *a*, side view; *b*, ventral view.



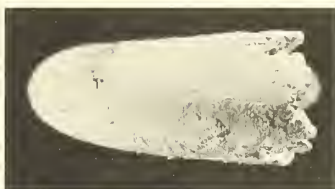
1a



2a



3a



1b



2b



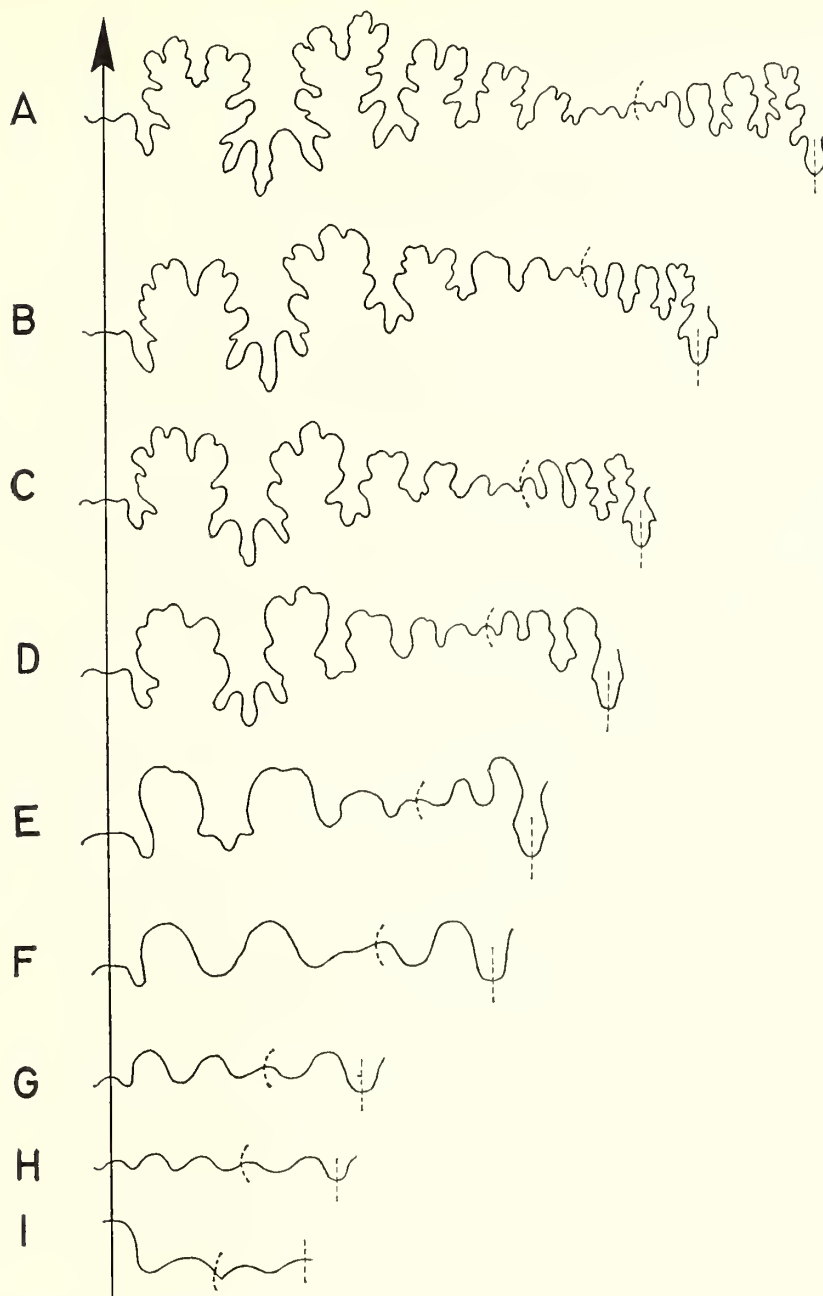
3b



4a



4b



TEXT-FIG. 12. Sutural ontogeny of *Creniceras renggeri* (Oppel). A, OUM J25244, $\times 12$ ($D' = 10.61$ mm.); B, OUM J25364, $\times 15$ ($D = 8.03$ mm.); C, OUM J25364, $\times 16$ ($D = 6.08$ mm.); D, OUM J25364, $\times 25$ ($D = 3.18$ mm.); E, OUM J25364 $\times 50$ ($D = 1.43$ mm.); F, OUM J25364, $\times 50$ ($D = 0.99$ mm.); G, OUM J25364, $\times 50$ ($D = 0.38$ mm.); H, OUM J25364, $\times 50$ ($D = 0.33$ mm.); I, OUM J25364, $\times 50$ ($D = 0.28$ mm.). H, primary suture. I, prosuture. All specimens from the Mariae Zone, Woodham.

Phragmocone. The nepionic constriction occurs at a diameter of between 0.53 mm. and 0.56 mm., compared with 0.52–0.56 mm. in *T. richei*. However, only three measurements of the nepionic constriction were available for *C. renggeri*, compared with ten for *T. richei*. The whorl shape (text-fig. 11) and sutural ontogeny (text-fig. 12) of *C. renggeri* vary within very similar limits to those of *T. richei* (text-figs. 7 and 8).

A complete lack of ornament occurs until a diameter of about 4 mm., where shallow, distant, radial, umbilical swellings develop. These swellings fade on the flanks and do not re-form on either the venter or ventro-lateral regions. These features are consistent with those recorded in *T. richei* at comparable diameters. The W/D, U/D, and HH/D ratios are identical to those of *T. richei* at similar growth stages (text-figs. 3, 4, and 5).

The final whorl of the phragmocone is, in most cases, seen only on removal of the body-chamber. Septation generally ceases at a diameter of 8–9 mm. The mean diameter at which septation ceases, in over two hundred adults, is 8.4 mm.: standard deviation (σ) is 1.1; coefficient of variation (V) is 12.8 (text-fig. 6). Specimen OUM J25246, with a maximum septate diameter of 17 mm., is almost certainly a very large adult *C. renggeri* (Pl. 50, fig. 5). However, variation in over two hundred specimens of *C. renggeri* is not continuous to such a large diameter, the range of continuous variation being 5–13 mm. (text-fig. 6), and it seems that the specimen in question is an extreme form.

The final whorl of the mature phragmocone is typically oppelid in character, being compressed and involute and with a narrow umbilicus. There are $4\frac{1}{2}$ – $5\frac{1}{2}$ complete whorls from the prosepium to the end of the phragmocone in adult specimens.

Radial umbilical swellings are developed, which fade on the flanks. These generally number about ten per whorl and are comparable with those, in number, direction, and nature, of *T. richei* at a similar diameter (Pl. 50, fig. 2a, c and cf. Pl. 50, fig. 1c). The ventro-lateral area is smooth, as is the venter, except on the final quarter whorl of adults, where feeble ventral tubercles are almost always developed. The tubercles become well-defined immediately before the beginning of the body-chamber (Pl. 50, figs. 2a, 3; Pl. 51, figs. 1a, 2a, b). Uncoiling of the umbilical seam in adults begins before the final septa are deposited (Pl. 50, figs. 2, 4, 5; and Pl. 52, figs. 2b, 3, 5), becoming markedly so on the body-chamber (Pl. 50, figs. 2a, 3; Pl. 51, figs. 2a, 3; Pl. 52, figs. 1, 3, and text-fig. 13).

Sutures were drawn at a diameter of approximately 8 mm. from nine specimens, showing the first and second lateral saddles and the ventral and lateral lobes. Differences in the same suture on either side of the venter are decidedly small (text-fig. 14); whereas

EXPLANATION OF PLATE 50

Fig. 1. *Taramelliceras richei* (de Loriol), OUM J25430. a, side view of adult phragmocone; b, ventral view of adult phragmocone; c, preparation of the inner whorls.

Figs. 2–4. *Creniceras renggeri* (Oppel). Fig. 2. OUM J25244. a, side view of adult specimen; b, ventral view of adult body-chamber; c, preparation of the inner whorls. Fig. 3. OUM J25360. Rostrate adult specimen. Fig. 4. OUM J25282. Body-chamber with almost complete peristome. a, side view; b, ventral view; c, apertural view.

Fig. 5. *C. renggeri* (?), OUM J25246. Giant adult male?

Specimens have been whitened with ammonium chloride. All from the Mariae Zone, Woodham, Bucks. All figs. $\times 3$.



1a



2a



2b



2c



1b



1c



3



4a



4b

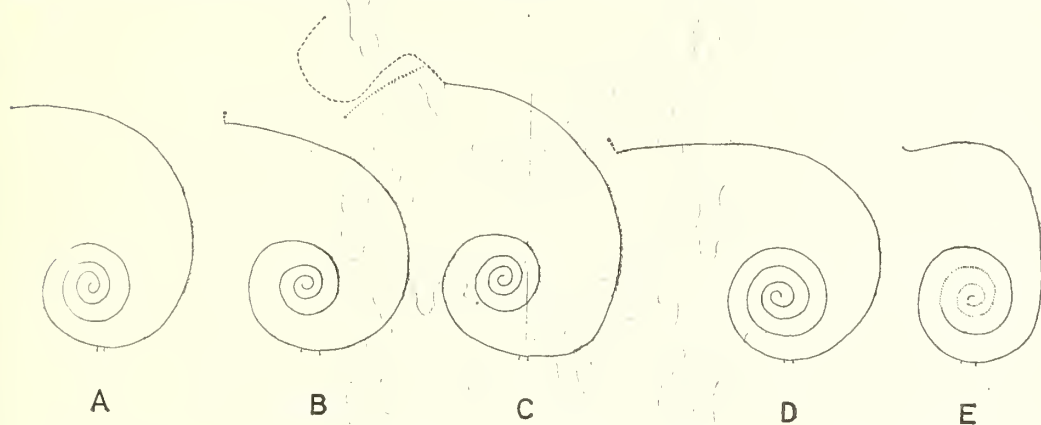


4c



5

differences between sutures of different specimens, drawn at approximately the same diameter, are more marked (text-fig. 15). The range of variation, qualitatively assessed, appears to be similar to that shown by *T. richei* (cf. text-figs. 9 and 10). Sutural approximation can clearly be seen in a large number of specimens (Pl. 50, figs. 2a, 3; Pl. 51, figs. 1a, 3a, 12; Pl. 52, figs. 2a, b, 3, 4, 5, 6).

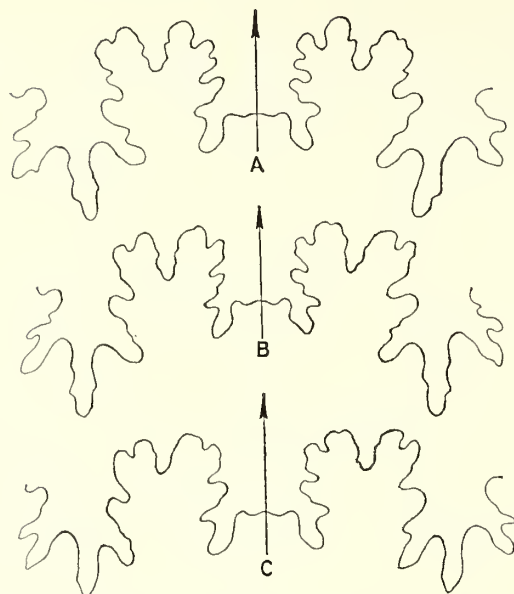


TEXT-FIG. 13. Diagrams of the umbilical seam of *Creniceras renggeri* (Oppel). The positions of the last two sutures are indicated. C, position of venter and lappet indicated. A, OUM J20662; B, OUM J20673; C, OUM J25364; D, OUM J20675; E, OUM J25377. All $\times 10$. All specimens from the Mariae Zone, Woodham.

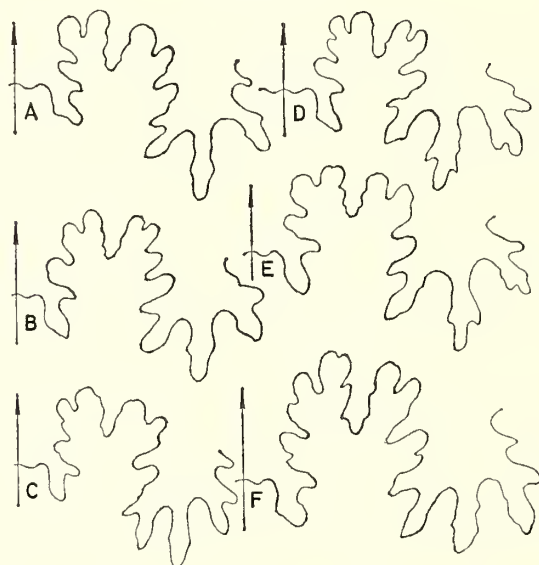
Body-Chamber. In nearly all specimens of *C. renggeri* a large proportion of the final whorl is body-chamber: in complete specimens the body-chamber occupies two-thirds to three-quarters of a volution (Pl. 51, figs. 2a, 4; Pl. 52, figs. 1-3, 5, 6). In complete adult specimens the total number of whorls, counting from the prosepium, is from $5\frac{1}{2}$ - $6\frac{1}{2}$. Morphology apart, the most striking difference between the body-chamber and phragmocone is that of colour. When pyritized the body-chamber is preserved as a golden reflective internal mould, whereas the phragmocone is a dull black colour. The body-chamber is frequently well preserved and some specimens have almost complete apertures.

Spiral striae are developed on the body-chamber of all adult specimens: this feature is particularly well seen on specimens OUM J25248, J25265 and J25392 (Pl. 51, fig. 3a; Pl. 52, figs. 2a, 6). The striation is only feebly developed on the phragmocone (Pl. 51, fig. 3a), if at all.

The ventral tubercles of the phragmocone give rise to large truncated spines on the venter of the adult body-chamber. A great deal of variation is to be seen between specimens concerning the spines. At one extreme a few specimens have perfectly smooth venters (Pl. 52, figs. 2, 4), while others develop enormous spines (Pl. 52, figs. 1, 5). Among the Woodham population, however, a complete range from smooth venters to coarsely spined ones is to be seen (Pl. 51, figs. 5-12 and Arkell 1939, pl. 9, figs. 15-27). The majority of specimens have spines similar to those of OUM J25392 (Pl. 52, fig. 6). In complete adults there are generally nine to twelve spines on the body-chamber; however, the total number depends largely on the size of the spines: specimens with finely denticulate venters having as many as twenty-four (Pl. 51, fig. 11).



TEXT-FIG. 14. Sutural variation in *Creniceras renggeri* (Oppel). A, OUM J25335 (D = 8.5 mm.); B, OUM J25327 (D = 8.0 mm.); C, OUM J25329 (D = 8.3 mm.). All $\times 15$. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 15. Sutural variation in *Creniceras renggeri* (Oppel). A, OUM J25367 (D = 7.8 mm.); B, OUM J25366 (D = 7.6 mm.); C, OUM J25326 (D = 7.8 mm.); D, OUM J25341 (D = 8.2 mm.); E, OUM J25345 (D = 8.2 mm.); F, OUM J25355 (D = 8.1 mm.). All $\times 15$. All specimens from the Mariae Zone, Woodham.

The general inclination of the spines is slightly rursiradial (Pl. 51, fig. 1*a*; Pl. 52, fig. 6); rectiradial direction is fairly common (Pl. 51, fig. 2*a*) and prorsiradial direction rare and, at best, very slight.

In all adult specimens which have a complete body-chamber the ventral spines fade out completely just before the aperture (Pl. 50, figs. 2*a*, 3, 4*a*; Pl. 51, figs. 2*a*, 4 and Pl. 52, figs. 3, 6). Spines may not develop near the aperture, or, if they do, they are formed as solid shell, a mould of which would not reflect their original shape. The final spine of OUM J20695, an incomplete adult, is truncated near the base (Pl. 51, fig. 5); obviously not broken, the spine may have formed as solid shell with only the lowermost part hollow.

On well-preserved spines, fine ridges can be seen parallel to the edge of the spine (Pl. 51, figs. 1*a*, *d*). Arising from the ventral spines in many individuals are sinuous ventro-lateral ribs, which often fade on the flanks and may, or may not, reappear weakly in the umbilical region (Pl. 51, fig. 1*a*). In specimens with a denticulate venter, these shallow ribs are better defined in the ventro-lateral region, weakening on the flanks and umbilical region (Pl. 51, fig. 11). Individuals with no spines rarely develop ribs; at best they are very feeble and atypically weakest in the ventro-lateral position (Pl. 52, figs. 2*a*, *b*, 4). Because of the shallowness and large width of the ribs, they are only seen in well-preserved specimens.

The peristome of adult specimens of *C. renggeri* develops constrictions, flares, lappets and rostra and is considerably more ornate than that of *T. richei*. Constrictions in adults vary from feebly developed to quite strongly so (Pl. 51, fig. 2*a*; Pl. 50, fig. 4*a*). In the case of well-developed constrictions the peristome is flared (Pl. 50, fig. 4*a*, *c*): however, the conditions of preservation may have been unfavourable for faithfully recording the true shape of both lappets and rostra in this species. Lappets are generally short, close to the umbilical seam and triangular to elongate in shape (Pl. 51, figs. 2*a*, 4; Pl. 52, figs. 2*b*, 3). Flattened specimens labelled *Ammonites cristatus* Sowerby, from the Oxford Clay of Scarborough, Yorkshire, though poorly preserved, show the lappets to be considerably more elongate than shown by the Woodham specimens (Pl. 52, figs. 7, 8). The preserved part of the lappet of OUM J25325 (Pl. 51, fig. 4) is identical to the early part of the lappet of BM C.27545 (Pl. 52, fig. 8): the lappet of the former is obviously broken and may well have been the same shape and size as that of the latter. The two forms (*A. cristatus* and *C. renggeri*) are probably conspecific, the Yorkshire individuals giving a truer outline of the lappet. In some cases the Woodham specimens have lappets which, in cross-section, are concave relative to the median plane (Pl. 50, fig. 4*c*; Pl. 51, fig. 2*b*). The rostra of Woodham specimens (Pl. 50, figs. 3, 4*a*; Pl. 51, figs. 2*a*, 4; Pl. 52, fig. 3) are almost identical with those of the Yorkshire specimens (Pl. 52, figs. 7, 8) in both size and inclination.

As on *T. richei* a line appears on the body-chamber of *C. renggeri* immediately after the last septum on adult specimens, possibly representing the position of the annulus (Crick 1898). The course of this line is almost identical with that recorded for *T. richei* (Pl. 51, figs. 10, 12). Faint muscle scars were seen on the venter of several individuals: they are particularly prominent in a smooth-ventered specimen, OUM J25376, where they occur immediately either side of the mid-ventral line in the earliest part of the body-chamber and extend adorally for about 50° of a volution (Pl. 52, fig. 4*a*, *b*).

DISCUSSION ON SEXUAL DIMORPHISM

De Blainville (1840) was the first author to point out the possibility of separate sexes in the ammonites. More recent work (Callomon 1955 and 1963; Makowski 1962) has shown that among synchronous large and small forms of initially identical ammonites, there is sound reason for accepting de Blainville's claim. By analogy with living cephalopods, the large form is thought to be the female and the small form the male: these are the macroconchs (M) and microconchs (m), respectively, of Callomon (1955 and 1963).

The present author accepts the criteria of Makowski (1962) relating to sexual dimorphism in ammonites:

- (1) identical initial stages of ontogeny in both (large and small) forms, and identity of their phylogeny,
- (2) lack of intermediate forms in adult (gerontic) stages,
- (3) presence of both forms in the same strata,
- (4) numerical ratio of the supposed sexes (sex ratio), comparable to that observed in living forms.

In the foregoing account it has been shown that *T. richei* and *C. renggeri* agree in early ontogenetic stages but it has yet to be shown that they can be 'phylogenetically identified'. As Callomon (1963) has pointed out; '[*Taramelliceras* and *Creniceras*] both commence together at the base of the Oxfordian, basal Mariae Zone (Renggeri Marls); both are there already very variable (see Arkell 1939), and I [Callomon] have the feeling that they are merely dimorphic companions thence throughout the rest of

EXPLANATION OF PLATE 51

Creniceras renggeri (Oppel) from the Mariae Zone, Woodham, Bucks.

Fig. 1. OUM J25245. Adult specimen. *a*, side view; *b*, apertural view; *c*, ventral view; *d*, ridges on ventral spines ($\times 10$). Fig. 2. OUM J25249. Adult with almost complete peristome. *a*, side view; *b*, apertural view. Fig. 3. OUM J25248. Adult specimen. *a*, side view; *b*, apertural view; *c*, ventral view. Fig. 4. OUM J25325. Adult specimen with almost complete peristome. Fig. 5. OUM J20695. Adult specimen showing truncated spine. Fig. 6. OUM J25252. Adult specimen. Fig. 7. OUM J25254. Adult specimen. Fig. 8. OUM J20662. Adult specimen. Fig. 9. OUM J25250. Adult specimen. Fig. 10. OUM J25250. Unwhitened adult specimen showing the course of the annulus (?). Fig. 11. OUM J25253. Adult specimen. Fig. 12. OUM J25255. Unwhitened adult specimen showing the course of the annulus (?). Specimens have been whitened with ammonium chloride, except figs. 10 and 12. Photographs by the author. All $\times 3$, except 1*d* which is $\times 10$.

EXPLANATION OF PLATE 52

Figs. 1-8. *Creniceras renggeri* (Oppel), from the Mariae Zone, Woodham, Bucks.

Fig. 1. OUM J25247. Adult specimen. Fig. 2. OUM J25265. Adult specimen with almost complete peristome. *a*, side view, showing spiral striae; *b*, side view, showing lappet. Fig. 3. OUM J25364. Complete adult specimen showing lappet and rostrum. Fig. 4. OUM J25376. Incomplete adult showing muscle scars. *a*, side view; *b*, ventral view. Fig. 5. OUM J25356. Almost complete adult specimen. Fig. 6. OUM J25392. Almost complete adult specimen. Fig. 7. BM 39644; Oxford Clay, Yorkshire. Complete specimen, probably an adult. Fig. 8. BM C.27545; Oxford Clay, Yorkshire. Complete specimen, probably an adult. Fig. 9. *C. renggeri* ♂ and ♀. Reconstruction: ♂ based on OUM J25392 and BM C.27545 (see figs. 6 and 8); ♀ based on OUM J25660 and BM 39642 (see Pl. 48, fig. 7). $\times 1$. Specimens have been whitened with ammonium chloride. Photographs by the author. All $\times 3$, except fig. 9 which is natural size.



1a



1b



1c



2a



2b



1d



3a



3b



3c



4



5



6



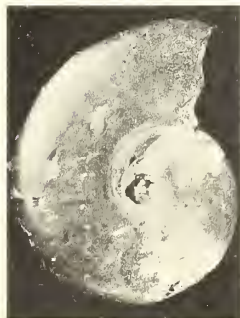
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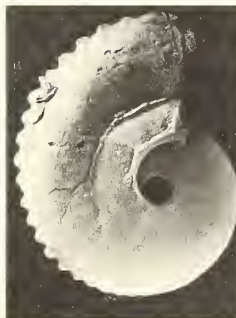
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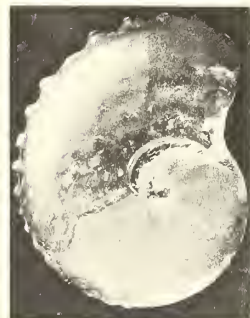
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10



11



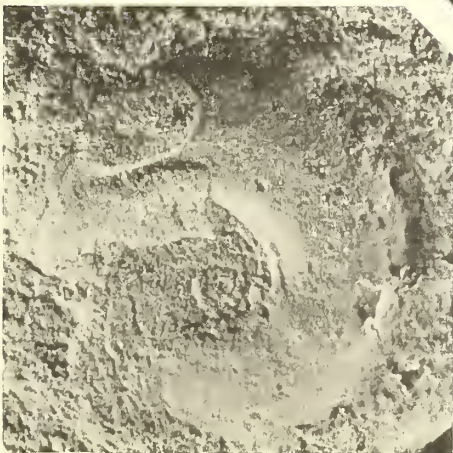
12



1



5



8



2a



2b



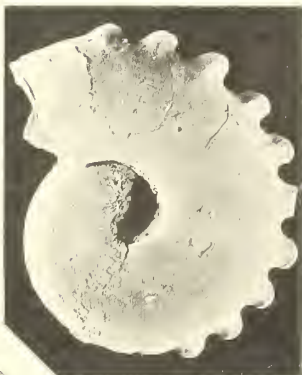
3



4a



4b



6



7



9

the Upper Jurassic.' Both *Taramelliceras* and *Creniceras* extend into the Kimmeridgian (Arkell 1957, p. L125; see Arkell, Kummel and Wright 1957; Hölder 1955 and Ziegler 1957 and 1959). As far as the author is able to determine, neither genus is found at higher levels than the Kimmeridgian.

Among the Woodham oppelids there are certainly no intermediates between *T. richei* and *C. renggeri*; there is a 'morphological hiatus' (Makowski 1962) of about one whorl of growth and the largest adult *C. renggeri* is not as large as the smallest *T. richei* (text-fig. 6). The two 'species' occupy the same strata, and, as far as can be determined, both begin at the same level, basal Mariae Zone, at Woodham.

The ratio of the large to small forms, *T. richei* to *C. renggeri*, is two to one. This can only be an approximate ratio as specimens from Woodham with a diameter of less than 8–9 mm. cannot reliably be differentiated into large and small forms. By analogy with living cephalopods, which show sexual dimorphism (Sweet 1964, p. K9; Makowski 1962, pp. 56–58), it is not unreasonable to contend that the two forms, *T. richei* and *C. renggeri*, are sexual dimorphs: they show sexual differences, both size and sex ratio, comparable with those displayed by living cephalopods. A reconstruction of the dimorphic pair has been produced (Pl. 52, fig. 9). It is to be inferred that the larger is the female.

TAXONOMY

The taxonomic problems, which acceptance of the sexual dimorphism theory bring, have been discussed at length by Callomon (1955 and 1963) and Makowski (1962). The present author is of the opinion that sexual dimorphs of the same species should have the same specific name (Makowski 1962), being differentiated by the zoological symbols ♂ and ♀. The specific name accepted for a dimorphic pair should be that of the first named 'species' (following the law of priority) and, as far as the author can assess, there should be no more complication in ammonite taxonomy than in, say, ostracod taxonomy where sexual dimorphs of the same species are given the same specific name.

Jeannet (1951) does not include the genus *Creniceras* Munier-Chalmas in the family Taramelliceratinae Spath 1928. The genus, along with *Bukowskites* nov. and *Popanites* Rollier, is classified by Jeannet as: 'Incertae Sedis', family Oppeliidae Bonarelli 1894. As the present results show, *C. renggeri* and *T. richei* are sexual dimorphs of the same species (= *C. renggeri*) and on this basis the author agrees with Arkell, Kummel and Wright's (1957) classification in which the genus *Creniceras* is included in the subfamily Taramelliceratinae.

SUMMARY AND CONCLUSIONS

Creniceras renggeri (Oppel) and *Taramelliceras richei* (de Loriol) from Woodham are identical in every feature up to a diameter of about 8 mm. In the late stages of the adult phragmocone, both 'species' develop feeble ventral tubercles which become ventral spines on the body-chamber. *T. richei* differs from *C. renggeri* in that ventro-lateral spines may be developed on the body-chamber.

The variation shown by the sutures at diameters of 8 mm. and 12 mm., in *C. renggeri* and *T. richei* respectively, is small and qualitatively similar. Sutural ontogeny is identical throughout: the sutures of *T. richei* become more complex in the adult stages, but always at larger diameters than are recorded for adult phragmocones of *C. renggeri*.

In adults the body-chamber of both 'species' uncoils at the umbilical seam. The peristome of *T. richei* is relatively simple; that of *C. renggeri* is ornate, developing flares, constrictions, rostra, and lappets.

Recent work has added substance to de Blainville's theory of sexual dimorphism in ammonites. By analogy with living cephalopods it seems probable that the large form is the female and the small form the male.

It is concluded that *Creniceras renggeri* (Oppel) and *Taramelliceras richei* (de Loriol) are really male and female respectively of the same species, and that the specific name of the dimorphic pair should be that of the earliest named form. It is finally considered that the inclusion of the genus *Creniceras* in the subfamily Taramelliceratinae is correct.

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THE LOWER LIASSIC AMMONITES *NEOMICROCERAS* GEN. NOV. AND *PARACYMBITES*

by D. T. DONOVAN

ABSTRACT. *Neomicroceras commune* gen. et sp. nov., family Eoderoceratidae, is described and figured from the Raricostatum Zone of the British Lower Lias. The genus *Paracymbites* Trueman and Williams 1927, from the same zone, is revised from the original types and other material, and placed in the family Oxynoticeratidae.

STUDY of the Lower Liassic ammonites from the Geological Survey borehole at Witney (Apley Barn), Oxfordshire, has led to the recognition of a new genus, here named *Neomicroceras*, and to the revision of another, *Paracymbites* Trueman and Williams, which was previously known only from a figure of the inner whorls. Both genera are now fully described and figured.

The following abbreviations are used: BM = Palaeontology Department, British Museum (Natural History). GSM = Geological Survey and Museum, London.

SYSTEMATIC DESCRIPTIONS

Order AMMONOIDEA

Family EODEROCERATIDAE Spath 1929

Subfamily EODEROCERATINAE Spath 1929

Genus NEOMICROCERAS gen. nov.

Type species. Neomicroceras commune sp. nov.

Diagnosis. Evolute ammonites of the family Eoderoceratidae with simple, radial ribs on the whorl-side. The ribs may bear small tubercles at their ventral ends. The suture-line is very simple: the saddles are broad, rounded, and never constricted at their bases; the external saddle is bifid or trifid, the other saddles are not normally divided. The genus is a homeomorph of *Crucilobiceras* but is distinguished from it by the different, much simpler suture-line and by the shorter smooth stage, up to 0.35 cm. diameter compared with about 0.5 cm. in *Crucilobiceras*. The single known species is small, never exceeding 20 mm. diameter.

Remarks. *Neomicroceras* is placed in the Eoderoceratinae on account of its similarity to the inner whorls of the less strongly ornamented species of *Crucilobiceras*. Its range, as at present known, lies entirely above that of *Crucilobiceras* and it could have evolved from that genus. No intermediate forms are known. The suture-line of *Crucilobiceras* passes through a stage similar to that of *Neomicroceras* during its ontogeny, as shown by Schindewolf (1962, text-figs. 107*b*, *c*). By a diameter of about 1.0 cm., however, the *Crucilobiceras* suture-line has many more indentations than that of *Neomicroceras* and [Palaeontology, Vol. 9, Part 2, 1966, pp. 312–18, pl. 53.]

the external and sometimes other saddles have constricted bases, a feature never observed in the new genus.

Other genera of Eoderoceratinae in the British Raricostatum Zone (*Eoderoceras*, *Bifericeras*) show sutural development and complexity very like that of *Cruciloboceras*.

Neomicroceras commune sp. nov.

Plate 53, figs. 1–4, text-fig. 1

Holotype. GSM 87550 from the Lower Lias of the Apley Barn Borehole, near Witney, Oxfordshire.

Paratypes. GSM 87551, 87553–6, from the same borehole as the holotype.

Other material. GSM 87557–60 from the Witney (Apley Barn) Borehole. Three specimens from the Dundry Borehole, Somerset, GSM 87561–3. Three specimens from Ballintoy, Co. Antrim, in the Ulster Museum and Art Gallery, Belfast, on a tablet numbered 674–1931. Geological horizon: In the Witney (Apley Barn) Borehole the genus ranges from 464 to 486½ ft. and lies entirely within the range of the ammonite *Leptechioceras*. It therefore occurs in the Macdonnelli Subzone of the Raricostatum Zone as currently defined (Dean, Donovan, and Howarth 1961, p. 460). The specimens from the Dundry Borehole are from the same subzone. The Irish specimens are not dated.

Description. The shell is evolute, with very little overlap between successive whorls. The largest individuals, around 16 mm. in diameter, consist of five and a half whorls. The first three whorls increase rapidly in size and the umbilicus is about 40 per cent. of the diameter at a size of 5 mm. On the last two and a half whorls the increase is more gradual and the umbilicus widens to about 52 per cent. at full size. The whorl height is about 27 per cent. of the diameter, and the whorl thickness 25 per cent. at full size.

The whorl side is smooth or faintly undulating to a diameter of about 35 mm. when regular ribbing begins. The rib-frequency rises from about 25 to the whorl at a diameter of 6 mm. to from 33 (holotype) to 40 (paratype no. 87554) at full size in the Witney (Apley Barn) material. Two of the Ballintoy examples have closer ribbing. They are provisionally regarded as individual variants as there is not enough material available to demonstrate the existence of a distinct, more closely ribbed species. The variation in rib-frequency within the Witney assemblage is normal for a Liassic ammonite species. The ribs are very slightly convex forwards and bear small tubercles at the ventral ends. All the Witney specimens are pyritized internal moulds but the Ballintoy examples retain the shell and show that the tubercles, blunt on the internal mould, are sharp on the shell. The Irish material also shows that the shell is striate between the ribs. In some individuals the ribs continue very faintly across the arched venter.

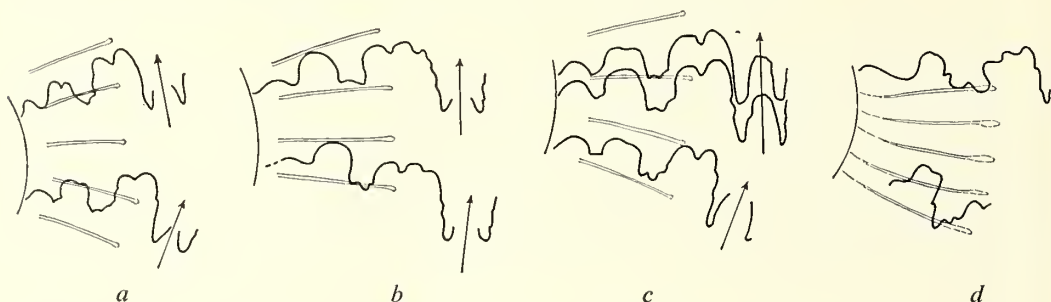
The body-chamber is about three-quarters of a whorl. Individuals retaining the body-chamber have the last two or three suture-lines approximated and are assumed to have been adult.

Examples of the external suture-line, which is the distinguishing feature of *Neomicroceras*, are shown in text-fig. 1. The external saddle is divided into two or three folioles. The other two saddles are normally broadly rounded but the larger sometimes shows incipient, and occasionally more distinct subdivision. This feature varies between successive suture-lines of the same individual (text-fig. 1a, c).

Family OXYNOTICERATIDAE Hyatt 1875
Genus PARACYMBITES Trueman and Williams 1927

Type species. Paracymbites obsoletus Trueman and Williams by original designation.

The holotype of the type species (GSM 51464) is from the Lower Lias of Stanton Fields cutting, about 10 miles north-east of Cheltenham, Gloucestershire (see Richardson, 1918, p. 17). The other fossils recorded from the cutting by Richardson indicate that the Oxynotum, Raricostatum, and Jamesoni Zones were exposed in the cutting, but there is no more precise information as to the horizon of the holotype.



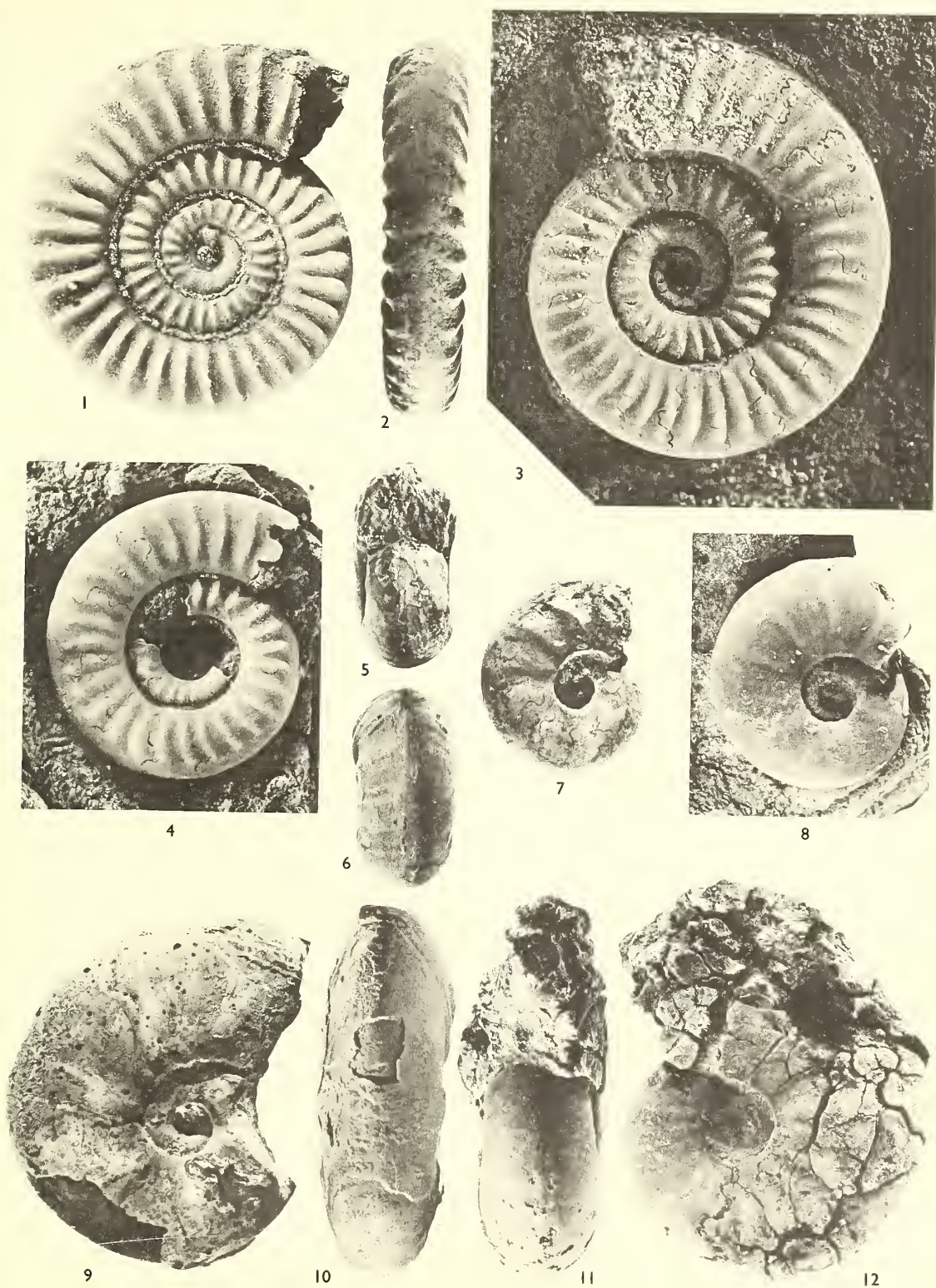
TEXT-FIG. 1. External suture-lines of *Neomicroceras commune* gen. et sp. nov. from the Lower Lias, Raricostatum Zone, of the Witney (Apley Barn) Borehole, Oxfordshire (a-c) and from Ballintoy, Co. Antrim (d). a, Paratype, GSM 87553; b, Paratype, GSM 87554; c, Holotype, GSM 87550, last three suture-lines; d, Ulster Museum and Art Gallery, 674-1931. Arrows mark mid-ventral lines. All $\times 8$.

Diagnosis. Small involute ammonites rarely exceeding 15 mm. in diameter. The earliest whorls have a roughly semicircular section; on the last whorl the whorl-section becomes parallel-sided with arched venter. Each whorl almost completely covers the preceding one. The umbilicus is about one-quarter of the diameter, and may open out slightly with the last whorl. Ill-defined simple folds or ribs are present on the whorl-side of some individuals. A very faintly marked keel may be present on the earlier part of the last whorl. The aperture is plain with a blunt ventral rostrum. The body-chamber is probably about three-quarters of a whorl. The external suture-line consists of three saddles each of broadly arched form with slight indentations. *Paracymbites* differs from other Lower Jurassic ammonites of broadly similar aspect as follows: *Protocymbites* (Hettangian) is distinguished by its stronger and more regular ribbing; *Cymbites* (Sinemurian) by its much more excentric coiling, the adult whorl-height being about 35 per cent. of the diameter compared with 45 per cent. in *Paracymbites*; *Metacymbites* (Pliensbachian)

EXPLANATION OF PLATE 53

Figs. 1-4. *Neomicroceras commune* gen. et sp. nov., Lower Lias, Raricostatum Zone, of the Witney (Apley Barn) Borehole, Oxfordshire. 1, 2, Holotype, GSM 87550, $\times 4$; 3, Paratype, GSM 87555, $\times 6$; 4, GSM 87559, $\times 4$.

Figs. 5-12. *Paracymbites dennyi* (Simpson), Lower Lias, Raricostatum Zone. 5-7, GSM 51464, the holotype of *P. obsoletus* Trueman and Williams, Stanton Fields cutting, Glos., $\times 4$; 8, GSM 87552, Witney (Apley Barn) Borehole, Oxfordshire, $\times 4$; 9, 10, GSM Zd 3034, Folly Lane Brickpit, Cheltenham, Glos., $\times 4$; 11, 12, GSM Zd 3035, the holotype of *P. undulatus* Trueman and Williams, Folly Lane Brickpit, Cheltenham, Glos., $\times 4$.



by more excentric coiling, more depressed body-chamber, and suture-line with constricted bases to the saddles; and *Onychoceras* (Upper Toarcian) by more excentric coiling and stronger ornament, and more deeply incised suture-line.

Paracymbites demmyi (Simpson)

Plate 53, figs. 5–12, text-fig. 2

Ammonites Demmyi Simpson 1843, p. 9.

Ammonites Demmyi Simpson 1855, p. 38.

Phylloceras Loscombi, Sowerby (*pars*); Blake 1876, p. 296.

Anmonites Demmyi Simpson 1884, p. 66.

Oxynoticeras demmyi, Simpson sp.; Buckman 1909, pp. 7b, c, pl. 7, figs. 1, 1a, 2, 3.

Cymbites sp. Richardson 1918, p. 17, pl. 2, fig. 31.

Oxynoticeras demmyi (Simpson) Buckman; Spath 1925, p. 111.

Paracymbites obsoletus Trueman and Williams 1927, p. 247, pl. 27, fig. 8a–c.

Paracymbites undulatus Trueman and Williams 1927, p. 248.

Cymbites? demmyi (Simpson); Howarth 1962, p. 104.

non Cymbites cf. *obsoletus* (Trueman and Williams); Schindewolf 1961, p. 214, pl. 30, figs. 14–16, text-figs. 18, 19.

Types. Syntypes are four pyritized internal moulds in Whitby Museum on a tablet numbered 470. Three were figured for the first time by Buckman (1909). The fourth, a nucleus 4 mm. in diameter still attached to matrix, is probably conspecific with the others. It has not been figured. Buckman wrote '1 and 2 agree with SIMPSON's measurement; but fig. 1 seems to agree best with his description: therefore it is presumably the holotype'. The present writer disagrees; for example, Simpson wrote '[height of the] outer whorl about $\frac{1}{2}$ the diameter', a statement which applies to Buckman's fig. 2 but not to his fig. 1. Howarth (1962) accepts the original of Buckman's fig. 1 as holotype or lectotype, and the present writer prefers to regard it as lectotype designated by Buckman.

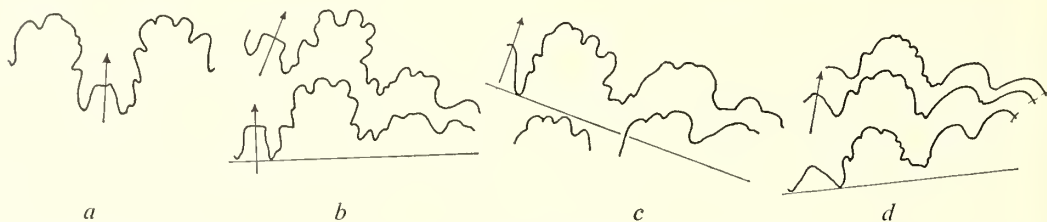
The holotype of *Paracymbites obsoletus* Trueman and Williams (1927), is in the Geological Survey Museum, no. 51464. It is refigured in the present paper, Plate 53, figs. 5–7. The holotype of *Paracymbites undulatus* Trueman and Williams is GSM Zd 3035. It has not been previously figured and is now shown in Plate 53, figs. 11, 12.

Other material. The species appears to be fairly common in the Lower Lias clays of Gloucestershire and Worcestershire and examples from various localities are preserved in the British Museum (Natural History) (nos. C6111a, C16666–9, C67060, and C67061) and in the Geological Survey Museum (nos. 24629, Zd 2954 (figured by Richardson, 1918, pl. 2, fig. 31), Zd 3034, Zd 3048, Zd 3072–4. The Witney (Apley Barn) Borehole yielded GSM 87552. The species does not appear to have been found on the Dorset coast.

Geological age. The horizon of *Paracymbites demmyi* in Yorkshire, as recorded by Simpson, would fall within the lower part of the Raricostatum Zone; Mr. L. Bairstow kindly informs me that he has not re-found the species during his work at Robin Hood's Bay. The Gloucestershire and Worcestershire specimens are not usually well dated, being finds from clay banks and spoil heaps. The Witney (Apley Barn) Borehole specimen comes from the Raricostatum Zone.

Description. The shell form has been described in the generic diagnosis. The coiling of the last whorl is excentric and variable; in some individuals, including the lectotype, the umbilicus opens out suddenly at the beginning of the last half-whorl, but in others, such as Buckman's fig. 2, this opening out is more gradual. The lectotype represents one extreme of variation in this character. The adult umbilicus varies between about 23 and 28 per cent. of the diameter (25 per cent. in the lectotype), and the whorl height just

behind the adult aperture is around 45 per cent. of the diameter. The shell may be almost smooth but is usually plicate, the folds—they are hardly ribs—having a slightly sigmoidal course following that of the growth-lines, and dying out half to two-thirds of the way from the umbilical suture to the mid-ventral line. The number of these folds varies



TEXT-FIG. 2. External suture-lines of *Paracymbites demmyi* (Simpson) from the Lower Lias, Raricostatum Zone, from the north end of the Hunting Butts tunnel, Cheltenham, Glos. (a), Folly Lane brick pit, Cheltenham (b, c), and the Witney (Apley Barn) Borehole, Oxfordshire (d). a, GSM Zd 3048; b, GSM Zd 3035, the holotype of *P. undulatus* Trueman and Williams; c, GSM Zd 3034; d, GSM 87552. Arrows mark mid-ventral lines. Straight lines are guide lines. All $\times 8$.

widely, from a few irregularly developed ones to over twenty to the whorl. The venter is obtusely angular for the first half of the last whorl but usually becomes rounded on the second half. On account of the frequency of specimens complete with body chamber about 15 mm. in diameter, the change in coiling which precedes the attainment of this size, and the absence of any larger specimens, a size of about 15 mm. was probably adult. Suture-lines are often irregularly spaced so that it is difficult to judge whether or not they are approximated before the body-chamber. The external suture-line (text-fig. 2) has three saddles on each side of the venter. The external one is roughly parallel-sided, and moderately indented; this character varies among individuals, and sometimes between the two sides of the same individual (text-fig. 2a). The other two saddles vary from being smooth (text-fig. 2d) to slightly indented (text-fig. 2b, c). The suture-line ascends towards the umbilical suture so that the lateral lobes lie well above the guide-line.

Synonymy. The holotype of *P. obsoletus* is wholly septate and only 8 mm. in diameter. The shell-form, ornament, and suture-line are sufficiently close to *P. demmyi* for *P. obsoletus* to be regarded as synonymous with Simpson's prior species. The other species placed in the genus by Trueman and Williams in 1927, *P. undulatus*, was not illustrated by them at the time. The holotype is now figured (pl. 53, figs. 11, 12) and is regarded as inseparable specifically from *P. demmyi*. Trueman and Williams did not say what they considered to be the differences between their two species.

Relationships and systematic position. The present writer is impressed by the similarity between *Paracymbites* and *Cheltonia*, an oxynoticeratid genus of the late Oxynotum Zone. *Cheltonia* is small (usually 25 mm. or less) and its affinities are beyond doubt, for it is almost indistinguishable from the inner whorls of *Oxynoticeratid* except for slightly excentric coiling and a modified body chamber. *Cheltonia* has in common with *Paracymbites*: change of whorl-section with growth, ornament on whorl side, aperture, and angular venter giving place to rounded on the last half-whorl. The main differences lie

in the greater whorl thickness of *Paracymbites*, and the absence of the corrugated venter which precedes the aperture in *Cheltonia*. On account of this close resemblance *Paracymbites* is placed in the family Oxynoticeratidae.

The similar genus *Cymbites* has been the subject of an exhaustive study by Schindewolf (1961), who regards *Paracymbites* as a synonym of *Cymbites*. The present writer disagrees with this view. In fairness it should be noted that *Paracymbites* is almost impossible to interpret from Trueman and Williams's original figures, and that the body-chamber, which provides the clearest difference from *Cymbites*, was not figured by them. Schindewolf figured three ammonites (1961, pl. 30, figs. 14, 15, 16a, b) as *Cymbites* cf. *obsoletus* (Trueman and Williams), but the present writer believes that they are not related to that species. The reasons for this are the coiling, which closely resembles that of *Cymbites* proper, and the ornament which passes undiminished in strength across the whorl-side on to the venter, a character of *Cymbites* (cf. Schindewolf's other figures of the genus) but not of *Paracymbites*.

Trueman and Williams did not place *Paracymbites* in a family, but suggested that it might be 'a dwarfed member of the Deroceratidae' [*recte* Eoderoceratidae] (1927, p. 248). In the Treatise (Arkell, 1957, p. L240) it was placed, as a subgenus of *Cymbites*, in the subfamily Cymbitinae Buckman 1919 of the family Arietitidae. Schindewolf (1961, p. 229) recognized a separate family Cymbitidae, *Paracymbites* being regarded as a synonym of *Cymbites*. I have remarked above that I disagree with Schindewolf on this point, and believe that his relegation of *Paracymbites* to the synonymy resulted from misidentification with that genus of German fossils which really belong to *Cymbites*. The present revision has shown that the closest similarities of *Paracymbites* are with *Cheltonia* and it is accordingly placed in the family Oxynoticeratidae and regarded as a homeomorph of *Cymbites*. I support Schindewolf in regarding the Cymbitidae as an independent lineage having its origin early in the Lower Lias; my earlier view (1957, p. 416) that *Cymbites* was evolved from *Euagassicerat* is not supported by evidence from recent boreholes.

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RADIOLARIA FROM THE NAMURIAN OF DERBYSHIRE

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ABSTRACT. *Albaillella pennata* sp. nov. and *Popofskyellum undulatum* Deflandre are described from calcareous concretions at the horizon of the goniatite *Reticoceras paucicrenulatum* Bisat and Hudson. The diagnosis of the genus *Albaillella* is emended. It is suggested that *A. pennata* and *P. undulatum* may possibly have been favoured by depths of water greater than those necessary for the proliferation of Namurian spumelline Radiolaria, and that depths favouring these two forms may have been attained only rarely during the deposition of Namurian goniatite bands in Derbyshire and Staffordshire.

THE occurrence of well-preserved Radiolaria associated with Namurian goniatites in North Staffordshire and South-west Derbyshire has been reported (Holdsworth 1964). The goniatites and Radiolaria are found in syndepositional calcite concretions—'bullions'—enclosed in shale, these bullions being closely comparable with the calcareous concretions of the Ohio Shale (Devonian) from which Foreman (1959, 1963) described rich radiolarian faunas.

The Namurian bullions appear to contain some of the best-preserved Carboniferous Radiolaria yet known, and other than the Ohio Shale occurrence, the faunas of some lower Viséan phosphatic nodules described by Deflandre (1946, 1952, 1958) and of some upper Viséan nodules (Demanet 1938), there are no records of Palaeozoic Radiolaria which can be studied in comparable detail. Palaeozoic Radiolaria are most commonly found in siliceous sediments and the faunas described only from thin-section studies (cf. Hinde 1899, Aberdeen 1940). Though the problem of separating the Namurian Radiolaria completely from the carbonate matrix has not been solved, nevertheless it has been possible to study many hundreds of excellent specimens on limestone surfaces etched with hydrochloric acid. In such preparations both external and internal structures can be determined more conveniently and with greater certainty than in thin-section.

Radiolarian faunas at sixteen successive goniatite horizons have been examined (cf. Holdsworth 1964), the zonal range being from low E₂b.1 to low R₂b, Arnsbergian Stage to mid-Marsdenian Stage, some two-thirds of the Namurian Series. The very great majority of the faunas are largely composed of spumelline forms belonging to the genera *Entactinia*, *Entactinosphaera*, and *Polyentactinia*. The detailed taxonomic work on these spumellines is still incomplete, but it seems clear that there is no obvious, regular change in species present from horizon to horizon comparable with the marked and irreversible trend of the successive goniatite faunas.

Differences which are seen between radiolarian faunas at different horizons, and between different collections from essentially the same horizon, are mainly ones of population density and of relative abundance of a few rather well-marked species. The form with the most notably fluctuating abundance, however, is the new species of the genus *Albaillella* (suborder Albaillellina) described below.

Non-spumelline Radiolaria are usually rare members of the Namurian faunas. *Albaillella pennata* sp. nov. has been found only at the horizon of *Reticuloceras paucicrenulatum* Bisat and Hudson, being abundant in two collections from a single locality but absent in two other collections from different localities. A closely related form, *Albaillella* aff. *pennata*, occurs at the lower horizon of *Homoceras subglobosum* Bisat. *Popofskyellum undulatum* Deflandre is very sparsely associated with *A. pennata* at the horizon of *R. paucicrenulatum* but has not been seen elsewhere.

Both the genera *Albaillella* and *Popofskyellum* were first described from the Viséan of the Montagne Noire and Cabrière. Neither genus has previously been described from other levels, nor from any British rocks.

SYSTEMATIC DESCRIPTIONS

Subclass RADIOLARIA Müller 1858

Order PORULOSIDA Haeckel 1887

Suborder ALBAILLELLINA Deflandre 1953

Diagnosis. Fossil Radiolaria with bilaterally symmetrical, elongate, siliceous shells, having a thin and usually imperforate wall and possessing internally non-axial rays—‘columelles’ (columellae) of Deflandre—eventually merging with the shell wall. Outside the shell is developed a skeleton, variable in detail.

Remarks. Deflandre (1952) suggested that a new order should probably be created for the genus *Albaillella*, but did not erect the order Albaillellidea until the following year (1953a). The order was defined fully by Deflandre in 1958 (p. 2278) and his diagnosis is quoted above. The Albaillellids are omitted by Campbell and Moore (1954) from the Treatise on Invertebrate Paleontology, Part D (cf. Deflandre 1960, p. 214), but in the framework of the Treatise classification it appears that the group should be considered as constituting a suborder rather than an order. In relegating the Albaillellidea to a suborder the present writer follows Foreman (1963, p. 285). (In Foreman (loc. cit.) the words ‘Suborder Albaillellina ? Deflandre 1953’ should appear immediately above the line ‘Family Albaillellidae ? Deflandre 1952’ (Foreman *in litt.* 1964).)

Two families, Albaillellidae and Lapidopiscidae (Deflandre 1958), are included in the Albaillellina. Whilst recognizing a very broad similarity of form and structure between the Albaillellidae, type family of the Albaillellina, and the Cyrtoidea, Deflandre (1952) considered the bilateral symmetry of the Albaillellidae to exclude them from the Cyrtoidea and from the Nassellina as a whole. This total separation of Albaillellina and Nassellina is accepted here, but it may be noted that rudimentary bilateral symmetry is expressed in the sagittal ring and spicule arrangement of some simple members of the Nassellina (cf. Campbell, *in* Campbell and Moore 1954, fig. 8) and that there is at least some analogy, possibly even homology, between the H-frame of *Albaillella* (cf. Deflandre 1952, fig. 5) and the spicular structures of simple members of the Nassellina with complete, unisegmental lattice shells. In the absence of demonstrable homologies, however, the Albaillellids are best considered as a separate suborder.

Family ALBAILLELLIDAE Deflandre 1952

Diagnosis. Fossil Radiolaria with thin, conical, bilaterally symmetrical, lamellar shells. Shells built on a framework of which the principal part, formed by two longitudinal

rods of dissimilar strength joined by a curved transverse bar (the H-frame), is exterior to the shell and opposite the basal aperture.

Remarks. The most characteristic feature of the family is the externally developed H-frame. The only known genus is *Albaillella*, though Foreman (1963) tentatively referred *Ceratoikiscum* Deflandre and *Holoeciscus* Foreman to the family.

Genus ALBAILLELLA Deflandre 1952

Type species. *Albaillella paradoxa* Deflandre.

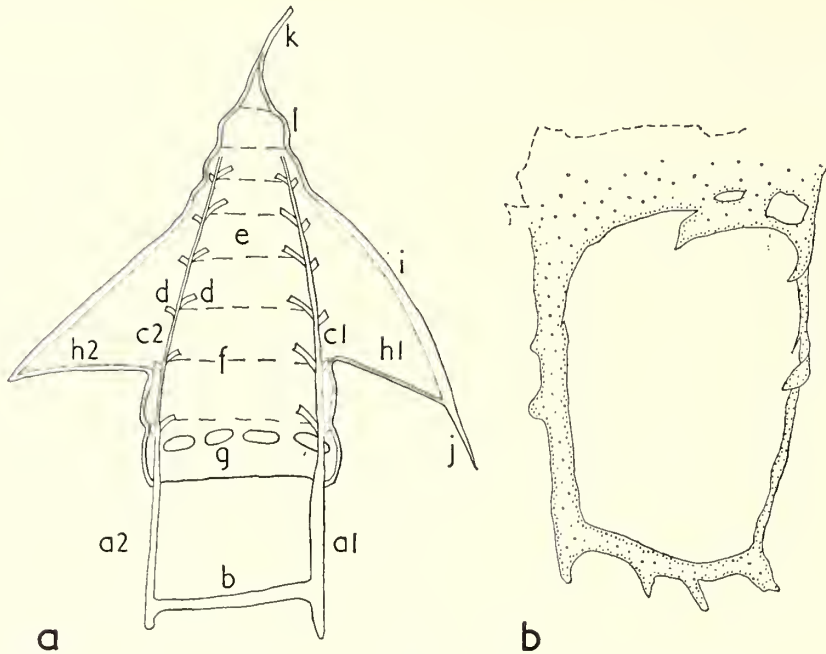
Emended diagnosis. Albaillellina in which the conical lattice shell may or may not be flattened bilaterally in the plane of the H-frame. Lattice shell may bear one or two hollow wings in the plane of the H-frame or may lack wings. Lattice shell sometimes shows a transverse segmentation or sometimes an oblique banding. Both rods of the external H-frame are produced into the interior of the lattice shell as longitudinal rays (columellae of Deflandre). They are of dissimilar strength, the stronger being developed from the stronger ray of the H-frame. The weaker (ventral) columella is sometimes indistinct. The stronger (dorsal) columella is usually attached to the inner surface of the lattice by paired lateral apophyses—'trabecules' (trabeculae) of Deflandre—and in some cases both rays are thus attached.

Remarks. Deflandre's several published accounts of forms attributed to *Albaillella* are not sufficiently detailed to establish the full variation encountered within the Viséan material with which he deals, or to decide how closely individual species agree with the original generic diagnosis. In the first publication on *Albaillella* (1952) a generic diagnosis is given, but no species names are mentioned in the text. Three species, *A. paradoxa*, *A. cornuata*, and *A. undulata*, and one variety, *A. paradoxa* var. *gibbosa*, are described only by drawings and named only in captions. The specific descriptions have not subsequently been amplified, though var. *gibbosa* was later given the status of a species (1960, p. 216, caption to pl. 1, fig. 23).

It is unclear from the published descriptions whether Viséan species of *Albaillella* invariably possess only a single columella—as appears to be the case in *A. paradoxa*, the type species (Deflandre 1952, p. 872, and fig. 4)—or whether both rods of the H-frame continue into the shell in the form of columellae, as is suggested by Deflandre (1953b, p. 408, fig. 307A, B). According to Deflandre (*in litt.* 1965) Viséan forms of the genus always, in fact, possess two columellae [as does the new Namurian species *pennata*] but the weaker (ventral) columella 'often shows a tendency to become effaced by inclusion in the shell wall'. Deflandre (*in litt.*) states that in Viséan species the stronger (dorsal) columella is 'often' attached to the shell wall by trabeculae, and that in 'some individuals' both dorsal and ventral columellae are so attached, the condition found in *A. pennata*. It should be noted that the columellae are simple continuations of the H-frame rods, not 'branches' from them as is suggested by the original description (Deflandre 1952, p. 872).

Clearly, the organization of the Namurian species is sufficiently similar to that of the Viséan forms for all to be included in a single genus. Apertural spines and an obliquely banded shell (cf. Deflandre 1953b, pp. 431–2) should not be considered as generic

features since they are not invariably present in Viséan species and are absent from the Namurian species.



TEXT-FIG. 1. *Albaillella pennata* sp. nov.

a, Diagrammatic representation of longitudinally bisected specimen to show the main architectural elements. *a1*, *a2*, dorsal and ventral rods of H-frame; *b*, cross-bar of H-frame; *c1*, *c2*, dorsal and ventral internal columellae; *d*, *d*, trabeculae; *e*, segment; *f*, constriction; *g*, pore; *h1*, *h2*, dorsal and ventral wings; *i*, wing rib; *j*, wing spine; *k*, apical spine; *l*, wall of lattice shell.

b, H-frame. Drawing from specimen, $\times 375$.

Anatomical nomenclature of Albaillella. The main architectural elements of frame and shell are illustrated diagrammatically in text-fig. 1. The side of the shell bearing the stronger columella is termed 'dorsal', as in the bicolumellate Lapidopiscidae (Deflandre 1958) which lack the H-frame. In *Albaillella pennata* the lattice shell is divided by transverse constrictions into a number of units and a similar, though less marked, partition of the lattice appears to be present in *A. undulata*. Each unit is here termed a 'segment', but the segmentation of the *Albaillella* lattice is not homologous with the segmentation in the Nassellina. In the Nassellina the first segment contains the spicular structures, if present, and these structures are thus isolated from all subsequent segments. Therefore, if the internal skeletal elements of the *Albaillella* are considered homologous with the spicular structures and sagittal ring of the Nassellina (see above), then the entire shell of *Albaillella* must be considered homologous with a single nasselline segment, comparable with the unisegmental lattice of the Archipiliidae.

The segmented lattice of *A. pennata* differs from the banded lattices (Deflandre 1952, p. 873; 1953b, p. 432) of *A. paradoxa* and *A. cornuata* in that the bands of these latter species are obliquely, not transversely, arranged. Thus portions of more than one band

are present at the periphery of the basal aperture in banded shells. In segmented shells the aperture is in a single segment.

The 'wings' of *A. pennata* are hollow portions of the lattice developed dorsally and ventrally, similar to the single outgrowth of the shell in *A. cornuata*, and differing from the 'horns' of *Lapidopiscum* (Deflandre 1958, p. 2279) in that they contain no portions of the columellae. It should be noted that Deflandre uses 'horn' in a quite different sense with respect to *Popofskyellum* (see below). In this case the horns are slender, solid, or hollow spines developed from the cephalis, not containing or continuous with columellae or spicules. These structures in *Popofskyellum* are therefore better termed simply 'cephalic spines'.

The outer margins of the wings in *A. pennata* are usually thickened to form longitudinal 'wing ribs' which may be produced beyond the tip of the wings as 'wing spines'. In his 'hypothetical reconstruction' of the *A. cornuata* frame Deflandre (1953*b*, fig. 307*A*) shows a lateral branch from the ventral columella in a position corresponding to the wing of *A. cornuata*. It is now known that there is no such connection between outgrowth and columella (Deflandre, *in litt.* 1965). The *A. cornuata* wing is comparable to the wings of *A. pennata* in that it is developed solely from the shell.

Albaillella pennata sp. nov.

Plate 54, figs. 1-3, 5-7

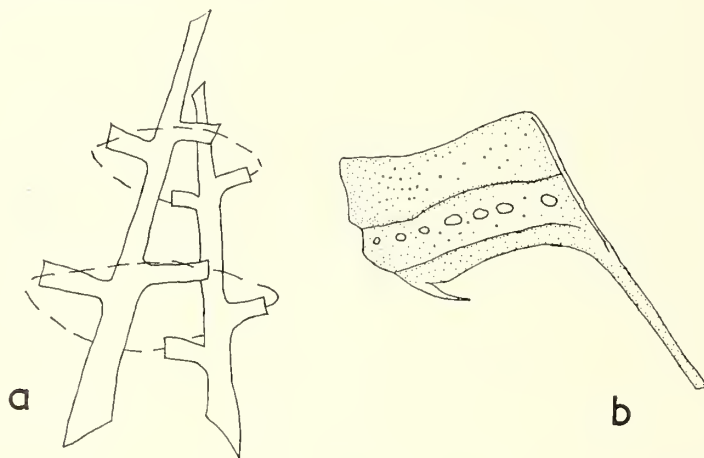
Winged nassellinid, Holdsworth 1964, p. 698.

Locality. Upper Dove Valley, South-west Derbyshire, England.

Horizon. Faunal band of *Reticuloceras pauciremulatum*, *Reticuloceras circumplacitile* Zone (R_{1a}), Kinderscoutian Stage (R₁), Namurian Series, Carboniferous.

Diagnosis. The shell bears prominent dorsal and ventral wings developed in a single plane, is conical from apex to the level of emergence of the wings, and tubular thereafter. In the most typical form the tubular portion of the shell constitutes about one-third of the total length, the overall outline being essentially triangular, but elongate variants occur in which the tubular portion may constitute half the length of the shell. Slightly oblique transverse constrictions divide the shell into segments and nine segments can be detected in complete specimens, though the first three are small and indistinct. A slender, slightly curved apical spine, hollow at the base, is developed from the first segment and there is generally a sudden increase in width of the lattice shell at the fourth segment. The wings arise most commonly at or about the level of the sixth segment and usually bear weak, longitudinal wing ribs, sometimes produced into wing spines. There is a general tendency for the dorsal wing to be developed slightly nearer the apex than the ventral wing. Both longitudinal rods of the H-frame continue into the shell interior as columellae, lying in the plane of the wings. The columellae are of markedly dissimilar strength, the stronger (dorsal) arising from the stronger rod of the H-frame. The columellae converge towards the apex of the shell, extending at least to the third segment and possibly to the apical segment. Along their entire length both columellae are attached to the adjacent lattice wall by pairs of small lateral branches (trabeculae), members of a pair being slightly offset vertically. The branches contact

the lattice shell at the constrictions (text-fig. 2a), and commonly there is indication of slight thickening of the shell along the apical sides of constrictions. The lattice shell is imperforate except for the final segment, where a girdle of irregular pores may be developed close to the constriction (text-fig. 2b). The transverse bar of the H-frame, only very rarely preserved completely in the available material, is slightly curved and ornamented with short spines (text-fig. 1b).



TEXT-FIG. 2. *Albaillella pennata* sp. nov.

a, Diagram showing relationship between constrictions of lattice shell (dashed lines) and trabeculae of the internal columellae.

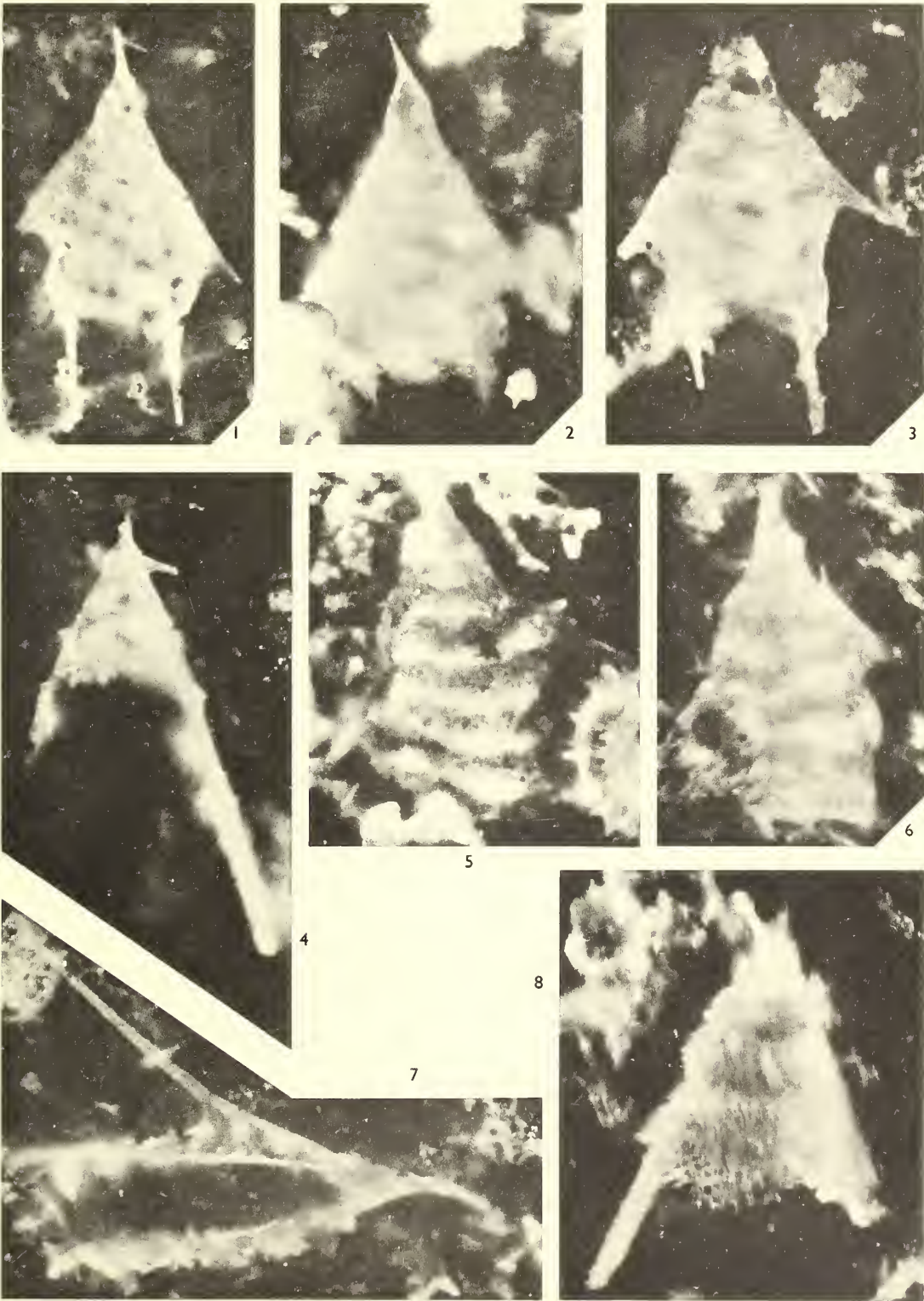
b, Final and penultimate segments with portion of dorsal rod of H-frame, showing girdle of irregular pores in final segment. Drawing from specimen, $\times 250$.

Variation. Specimens assigned to *A. pennata* are somewhat variable. The most distinct variant is an elongate form in which the tubular portion of the shell is up to half the total shell length and the wing spines are very long, extending to or beyond the level of the mouth. In the typical triangular form there is variation in the degree to which the segments are defined, in the development of wing ribs and wing spines, and in the size and position of the wings. In an extremely rare variant the development of the ventral

EXPLANATION OF PLATE 54

All figures $\times 250$.

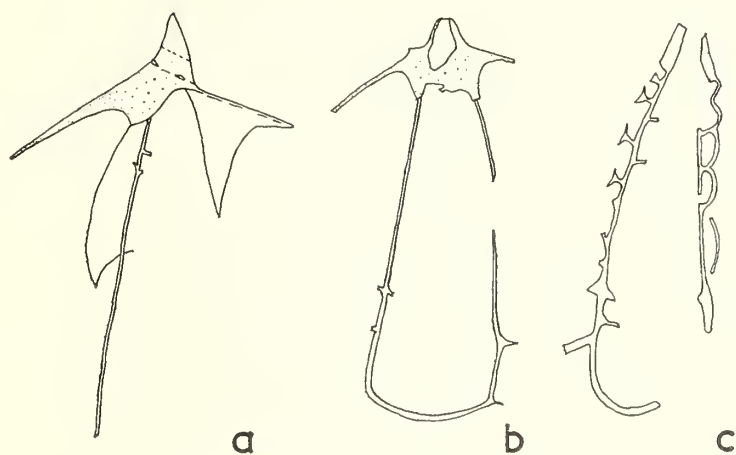
Figs. 1-3, 5-7. *Albaillella pennata* sp. nov. 1, Holotype, LZ 3651. 2, Topotype, LZ 4740, showing segmentation and incomplete apical spine. 3, Topotype, LZ 4739, showing marked inequality in strength of rods of H-frame and difference in level of the wings. 5, Paratype, LZ 3652, showing very well-marked segmentation. 6, Topotype, LZ 4737, elongate form showing segmentation and portion of wing spine. 7, Paratype, LZ 3653, elongate form with wing rib produced into long wing spine. Figs. 4, 8. *Popofskyellum undulatum* Deflandre. 4, Very incomplete specimen showing one lateral cephalic spine and the stronger of the two longitudinal ribs, LZ 4738. 8, Specimen showing the widely conical, segmented lattice of undulose outline, one lateral cephalic spine, and the stronger of the two longitudinal ribs, LZ 4736.



HOLDSWORTH, Namurian radiolaria

wing is delayed until the final segment. Occasionally pores are present in both final and penultimate segments, and some specimens lack pores completely.

Material. Deposited at the Geological Survey, Leeds. Holotype, LZ 3651 (Pl. 54, fig. 1), typical triangular form, but with segmentation rather weakly developed; length from tip of apical spine (probably broken) to base of dorsal rod of H-frame 0.24 mm. LZ 3658 is closely comparable with the holotype. Paratype, LZ 3652 (Pl. 54, fig. 5) and LZ 3654 show typical triangular shape with well-developed segmentation. LZ 3657, typical form, laterally broken, showing columellae internally. LZ 3655, triangular form with ventral wing weak, delicately spined and developed closer than usual to mouth. Paratype, LZ 3653 (Pl. 54, fig. 7), extreme elongate form with long wing spine; length from tip of apical spine (probably broken) to damaged aperture 0.31 mm. LZ 3656, specimen with shape intermediate between typical and elongate forms, having very weak ventral wing with strong, curved spine. Specimens cited are on the etched surfaces of two small slabs of limestone, and detailed instructions for locating specimens are deposited with the material. Figured specimens not cited above also have Geological Survey, Leeds, registration numbers.



TEXT-FIG. 3. *Albaillella* aff. *pennata* sp. nov. Drawings from specimens. *a*, Broken specimen showing apex of lattice shell with wings and one internal columella with remnants of trabeculae, $\times 203$. *b*, Broken specimen showing complete H-frame, two internal columellae and wings, $\times 180$. *c*, Broken specimen with only fragments of lattice shell, showing part of H-frame, and two internal columellae bearing remnants of trabeculae, $\times 164$.

Remarks. *A. pennata* differs from the four Viséan species of *Albaillella* so far described in possessing two wings and a rather markedly segmented shell. It differs also in that specimens invariably show a well-differentiated ventral columella bearing trabeculae.

A. pennata has been seen only at the horizon of *R. paucicrenulatum*, but poorly preserved specimens of a closely related form, determined as *A. aff. pennata*, are present at the lower horizon of *Homoceras subglobosum* Bisat. In *A. aff. pennata* (text-fig. 3*a-c*), as in *A. pennata*, there are two columellae, both bearing trabeculae, but the shell is more slender and less obviously segmented, and the two wings are smaller and set more closely to the apex.

Suborder ? NASSELLINA

Family POPOFSKYELLIDAE Deflandre 1964

Diagnosis. Fossil Radiolaria with a perforated, bell-shaped shell in which two opposed, longitudinal, lateral rods are incorporated. Cephalis simple. Podome with two branches.

Remarks. Though the greater part of the shell has a bilateral symmetry Deflandre (1964) excluded the family from the Albaillellina on the grounds that the arrangement of cephalic spines lacks this symmetry. The family differs also in having a perforate shell and lacking internal columellae, the longitudinal ribs being integral parts of the shell, homologous with the wing ribs of *A. pennata*. In the Namurian examples seen these longitudinal ribs or rods are of unequal strength.

Genus POPOFSKYELLUM Deflandre 1964

Type species. *Popofskyellum pulchrum* Deflandre (1960, pl. 1, fig. 26).

Diagnosis. Shell perforated, bell-shaped or conical, with two opposed lateral ribs or rods, usually projecting at the base. Podome with two branches. Cephalis with unbranched spines, frequently with a short, conical, tricostate spine. Poorly known, asymmetrical trabecular system basally.

Popofskyellum undulatum Deflandre

Plate 54; figs. 4, 8

Popofskyellum undulatum Deflandre 1964, pp. 3055–8; figs. 3, 4, 13, 14.

Remarks. All five incomplete Namurian specimens of the genus so far seen agree closely in size and architecture with *P. undulatum*, described by Deflandre from the Viséan. The most complete specimen (Pl. 54; fig. 8) has a cephalis and five other rather well-marked segments as in the holotype (cf. Deflandre 1964, fig. 14), giving the characteristic undulose outline to the shell, which is finely perforated overall and of muslin-like texture. The longitudinal rods of unequal strength arise in the region of the second extra-cephalic segment and extend beyond the periphery of the mouth. The total number of lateral cephalic spines cannot be determined, but there is at least one per specimen, and also a slender apical spine.

Popofskyellum is very rare in the Namurian faunas studied, being seen only at the horizon of *R. paucicrenulatum*, where it is associated with abundant specimens of *A. pennata*. The genus also appears to be rare in the Viséan faunas, for Deflandre's four species are based on a total of only about twenty specimens (Deflandre 1964, p. 3055).

ECOLOGY OF ALBAILLELLA PENNATA

Foreman (1963, p. 267) noted marked differences in relative abundance and morphology of radiolarian species between three concretions studied, all collected at 'approximately the same horizon' and separated by a total horizontal distance of only some four miles. The radiolarian faunas of the *R. paucicrenulatum* faunal band provide an even more striking example of apparent lateral variation at a single horizon.

The band was studied at three localities. At locality 1 in the Upper Dove Valley (loc. 179 of Holdsworth 1963) two bullions with *R. paucicrenulatum*, at exactly the same level, 1 foot apart horizontally, contained rich spumelline faunas abundantly associated with *A. pennata* and with very rare *P. undulatum*. Both these forms were completely absent from a bullion with the same goniatite at locality 2, 20 yards away and also from a fourth bullion with the goniatite at locality 3, 1 mile away in the Upper Manifold Valley (loc. 177 of Holdsworth 1963), which contained a rich but exclusively spumelline fauna. The possibility that the bullions at the three different localities are parts of three, vertically separated goniatite bands is remote. The goniatites present in all four collections are typical forms of *R. paucicrenulatum* (Holdsworth 1963, pp. 142–4) and in no known succession is this species seen to occur more than once. It must be accepted that the four bullions consist of sediment deposited during the single relatively brief time span marked by the existence in the area of *R. paucicrenulatum*.

This is not to say, however, that the two bullions from locality 1 and those from localities 2 and 3 constitute precisely contemporaneous sediment samples, even though the majority of faunal bands in this portion of the succession average only a foot or so in thickness. From the perfect three-dimensional preservation of goniatites in bullions it is clear that these concretions grew very early in diagenesis, before the oozes and muds had suffered any appreciable compaction. To judge by the total crushing of many globose goniatites in Namurian shale bands, an inch of shale must represent many inches of original sediment, and at the time the bullion concretions formed it seems probable that many inches, even feet, of highly water-charged mud and ooze were present below the sediment-water interface. As the *R. paucicrenulatum* bullions are relatively small, approximately seven inches deep at maximum, it is possible that the two bullions of locality 1 and those of localities 2 and 3 developed at three slightly different levels in the single sheet of sediment containing *R. paucicrenulatum*.

Thus there is a high probability that the variation between faunas at the three localities is a vertical, not a true lateral, variation. During the single time span marked by the existence of *R. paucicrenulatum* there were probably at least two distinct periods, one in which *A. pennata* coexisted abundantly with the goniatite and spumelline Radiolaria, and one in which only the goniatite and spumellines were present in the area.

To suppose that this indicates an extremely brief stratigraphical range for *A. pennata* is unrealistic in view of the evidently long ranges of the spumelline species and the presence of the closely comparable *A. aff. pennata* at a single lower horizon. The most reasonable explanation is that the occurrence of *A. pennata* was controlled by environment, and it is significant that *Popofskyellum* occurs only in association with *A. pennata*. Though probably not closely related phylogenetically, there are obvious similarities between the conical, bilaterally symmetrical genera *Albaillella* and *Popofskyellum*, and Deflandre (1964, p. 3057) suggested an evolutionary convergence in morphology. If the appearance of *A. pennata* was due to environmental change, then we must suppose, in view of the rarity of faunas including *Albaillella*, that the change taking place during '*R. paucicrenulatum* time' was somewhat unusual in the histories of the goniatite bands of Derbyshire and Staffordshire.

In considering the nature of this change it is significant that whilst *A. pennata* is extremely abundant in the bullions of locality 1, all the common spumellines of other horizons are also present in considerable numbers. The change in environment had no

effect upon the spumellines or the goniatites. The appearance of the two non-spumelline species could have been the result of several kinds of influence, of a minor change in salinity or temperature, or possibly a slight alteration in the speed of water movement. Such explanations presuppose that the spumellines were less sensitive to their immediate environment than *A. pennata* and *P. undulatum*. A rather more satisfactory explanation is that the two non-spumellines are relatively deep-water forms and were favoured by depths only seldom attained during the deposition of the Namurian goniatite bands studied. During the brief period of deeper water conditions favouring these two forms the free-swimming goniatite and the spumellines floating at relatively shallow depth could also flourish.

Potts (1960) adduced geochemical arguments for fluctuating sedimentation rates in at least one Namurian goniatite band, and it is possible that such changes in rate of sedimentation were linked to depth fluctuations of the kind now suggested for the *R. paucicrenulatum* band. The suggestion that *A. pennata* and *P. undulatum* are indicators of relatively deep-water conditions is at least in accord with the little yet known concerning modern radiolarian ecology and functional morphology. Both *Albaillella* and *Popofskyellum* possess shells superficially similar to those of many members of the Nassellina, and Haeckel (1887, p. cliv) believed nassellines to increase in abundance with depth in modern oceans and to predominate in the abyssal zone. Delicate lattice shells and elaborate spines amongst the Spumellina are probably adaptations to pelagic existence (cf. Aberdeen 1940), and whilst the Namurian spumellines show many examples of such structures (Holdsworth 1964), neither *A. pennata* with its dense, only slightly perforate shell, nor *P. undulatum* have any features which might suggest that they are highly adapted to a free-floating life in surface or immediately sub-surface currents. Both may even have been benthonic forms. The possibility of deep-water control is also in accord with the presence of *Albaillella* and *Popofskyellum* in the phosphatic Viséan nodules studied by Deflandre, sediments likely to have formed at considerable depth under conditions of reduced sediment accumulation.

Acknowledgements. I am indebted to Mrs. Helen P. Foreman (Oberlin College, Ohio) and Miss Catherine Clark (Scripps Institute of Oceanography, La Jolla) for helpful discussion, and to Prof. G. Deflandre (Laboratoire de Micropaléontologie, Paris) for unpublished information regarding *Albaillella* in the Viséan.

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A NEW ODONTOPLEURID TRILOBITE GENUS FROM THE DEVONIAN OF BOHEMIA

by DAVID L. BRUTON

ABSTRACT. A new odontopleurid genus *Isoprusia* (type *I. mydlakia* sp. nov.) is described and assigned to the subfamily Miraspidinae R. and E. Richter, 1917. The new genus includes *Odontopleura laportei* Hawle and Corda, *Acidaspis ursula* Barrande, ? *A. sperata* Barrande, *A. (Ceratocephala) sandbergeri* R. and E. Richter, *Orphanaspis cornuticauda* Erben, and *Koneprusia pennata* Lütke. Features of the pygidium of the new genus enable it to be distinguished from *Koneprusia* Prantl and Přibyl 1949, the type material of which cannot be traced. *Odontopleura subterarmata* Barrande, is tentatively retained in the genus *Koneprusia*. The type, and where possible, topotype material of these species is redescribed and figured. Evidence from the thorax of *Isoprusia* indicates that, in the pleural field and spines, considerable morphological modification can exist between the first formed (anterior) and last formed (posterior) segments. The relationship of the new genus to one or both of the *Miraspis-Ceratocephala* root stocks has been briefly discussed. A reconstruction of *Isoprusia mydlakia* is given.

DURING a visit in 1963 to the Geological-Paleontological Museum at the University of Marburg, West Germany, I found amongst the collections some well-documented odontopleurid material collected by the late Professor J. Jahn, from the Devonian Limestones of Bohemia. It seems likely that the material came to Marburg to be identified by the late Dr. Fr. Drevermann, who examined specimens for Professor Jahn on other occasions (see Jahn, 1903, p. 23, footnote).

Preparation of the soft, yellow, argillaceous limestone, revealed numerous well-preserved cranidia, pygidia, thoracic segments and hypostomata, either retaining the entire exoskeleton, or partly exfoliated. All the exoskeletal parts are thought to represent one new species, *Isoprusia mydlakia*, the type selected for the new odontopleurid genus *Isoprusia*.

The excellent preservation and abundance of the material has allowed a fairly full diagnosis to be given, and because of this, it has been found that some of the species formerly assigned to *Koneprusia* by Prantl and Přibyl (1949), are best placed in the new genus as here defined.

Visits to Museums in Czechoslovakia (1962), West Germany (1963), and the United States of America (1964) have allowed me to study types and additional material of all these species.

Acknowledgements. I am indebted to the following persons for so kindly allowing me to study the odontopleurid material in their care: Dr. Ronald Huckriede, Geological-Paleontological Institute, Marburg University (Mbg.), Dr. V. Zázvorka and Dr. Radvan Horný, National Museum, Prague (N.M.P.), Professor O. H. Schindewolf, Geological-Paleontological Institute, Tübingen University (T.U.), Dr. R. Heineck, Paleontological Department, Natural History Museum, Wiesbaden, and Professor Harry B. Whittington, Museum of Comparative Zoology, Harvard University (M.C.Z.). At Bonn in 1963, Dr. F. Lütke generously made available to me all of his recent collections from the Harz region along with types on loan from the Geological-Paleontological Museum, Humboldt University, East Berlin (H.U.). Mr. Jiří Vaněk and Dr. Ivo Chlupáč (Prague) have been most helpful in personal correspondence with regard to stratigraphic problems, and both have sent casts of their material. It gives me great pleasure in thanking Professors Whittington and P. C. Sylvester-Bradley

for reading the manuscript and for all their help and encouragement during its preparation. Mrs. E. K. Harris (Leicester) kindly prepared the text-figure from my original reconstruction.

This work has been made possible with the help of a D.S.I.R. studentship which I gratefully acknowledge.

Terminology and techniques. The terminology used is that recommended by Whittington (1956a), but I have followed Jaanusson (1956, pp. 36–37) in using the terms rachis (= axis) and dorsal furrow (= axial furrow); and in numbering and lettering the glabellar lobes (L) and furrows (S), from the posterior forwards. Before making the photographs, each specimen was coated with a dilute 'Opaque', and then lightly coated with ammonium chloride in the manner described by Whittington (1963, 'Explanation of Plates' following p. 118). The orientation of the specimens is that used by Whittington.

SYSTEMATIC DESCRIPTIONS

Family ODONTOPLEURIDAE Burmeister 1843

Subfamily MIRASPIDINAE R. and E. Richter 1917

Genus ISOPRUSIA gen. nov.

Derivation of name. Greek *Isos*, equal: *prusia*, suffix from Koněprusy, a small village in Bohemia.

Type species. *Isoprusia mydlakia* gen. et sp. nov.

Diagnosis. Cephalon rectangular in outline, cranium trapezoidal; frontal glabellar lobe expanded laterally. Two pairs of lateral glabellar lobes well defined. Occipital ring strongly convex medially, with median spine which may rise straight upwards or curve backwards distally. Posterior band may or may not be obviously separated by weak furrow from remainder of ring. Eye ridge weakly convex, positioned on outer part of inflated fixed cheeks. Palpebral lobe short, with well-defined palpebral furrow; eye ovoid, non-stalked. Anterior suture gently curved forward outside and almost parallel to eye ridge. Posterior suture directed outwards and backwards approximately in line with anterior suture, and crossing posterior border so as to produce ear-like projection of the latter which is widest at the suture.

Free cheek as in *Ceratocephala*, with straight anterior and sigmoidal lateral outline; lateral margin considerably widened. Border with short peg-like spines directed outwards and downwards. Librigenal spine with origin inside posterior margin.

Hypostoma subquadrate, anterior margin gently curved convexly outwards; posterior margin with deep narrow median notch and lateral ears. Median body shield-shaped, gently convex; border furrow running from inside antero-lateral margins. Deepened notches may be present at antero-lateral parts of median body. Small anterior wings, lateral shoulder, and lateral notch.

Thorax of ? ten segments. Pleurae with flattened central ridge which may be weakly furrowed or smooth. Band produced into two spines, the terminal downwardly directed spine blade-like with secondary spines from edges, and the principal pleural spines apparently directed outwards and upwards on anterior segments, becoming progressively curved upwards and backwards on posterior segments.

Pygidium semicircular in outline. Rachis not reaching posterior border, composed of two obvious rings and sometimes a lower terminal portion. Principal border spine

connected to weakly raised ridge which curves backwards from first ring. Secondary border spines lacking or numerous, small downwardly directed from postero-lateral margin.

Exoskeleton granulate or finely spinose.

Discussion. The following species are now assigned to the new genus. *Acidaspis ursula* Barrande 1872, *Odontopleura laportei* Hawle and Corda 1847, *Orphanaspis cornuticauda* Erben 1952, *Acidaspis (Ceratocephala) sandbergeri* R. and E. Richter 1917, ? *Acidaspis sperata* Barrande 1872, and *Koneprusia pennata* Lütke 1965.

Geological range. The genus is known from the Lower Devonian (Pragian-Emsian) and Middle Devonian (Eifelian) in Bohemia; Lower Devonian (lower-upper Emsian) and Middle Devonian (Eifelian-Givetian) in Germany; Middle Devonian (Couvinian) in Poland, and Middle Devonian of Kazakhstan, U.S.S.R.

Isoprusia mydlakia sp. nov.

Plate 55, figs. 1–20; Plate 56, figs. 1–16; Plate 57, fig. 13

Derivation of name. From the word *mydlak*, a Bohemian quarry term for soap-stone.

Holotype. Mbg. 398, Plate 1, figs. 1, 3, 4, 10, 11. Geological–Paleontological Institute, Marburg University.

Paratypes. Mbg. 399, Plate 55, figs. 2, 5, 7; Mbg. 400, Plate 55, fig. 8, Plate 57, fig. 13; Mbg. 401, Plate 55, figs. 6, 14, 18; Mbg. 402, Plate 55, figs. 12, 13; Mbg. 403, Plate 55, fig. 19; Mbg. 404, Plate 55, figs. 15, 20; Mbg. 405, Plate 55, fig. 16; Mbg. 406, Plate 55, fig. 17; Mbg. 407, Plate 55, fig. 9; Mbg. 408–16, Plate 56, figs. 1–16.

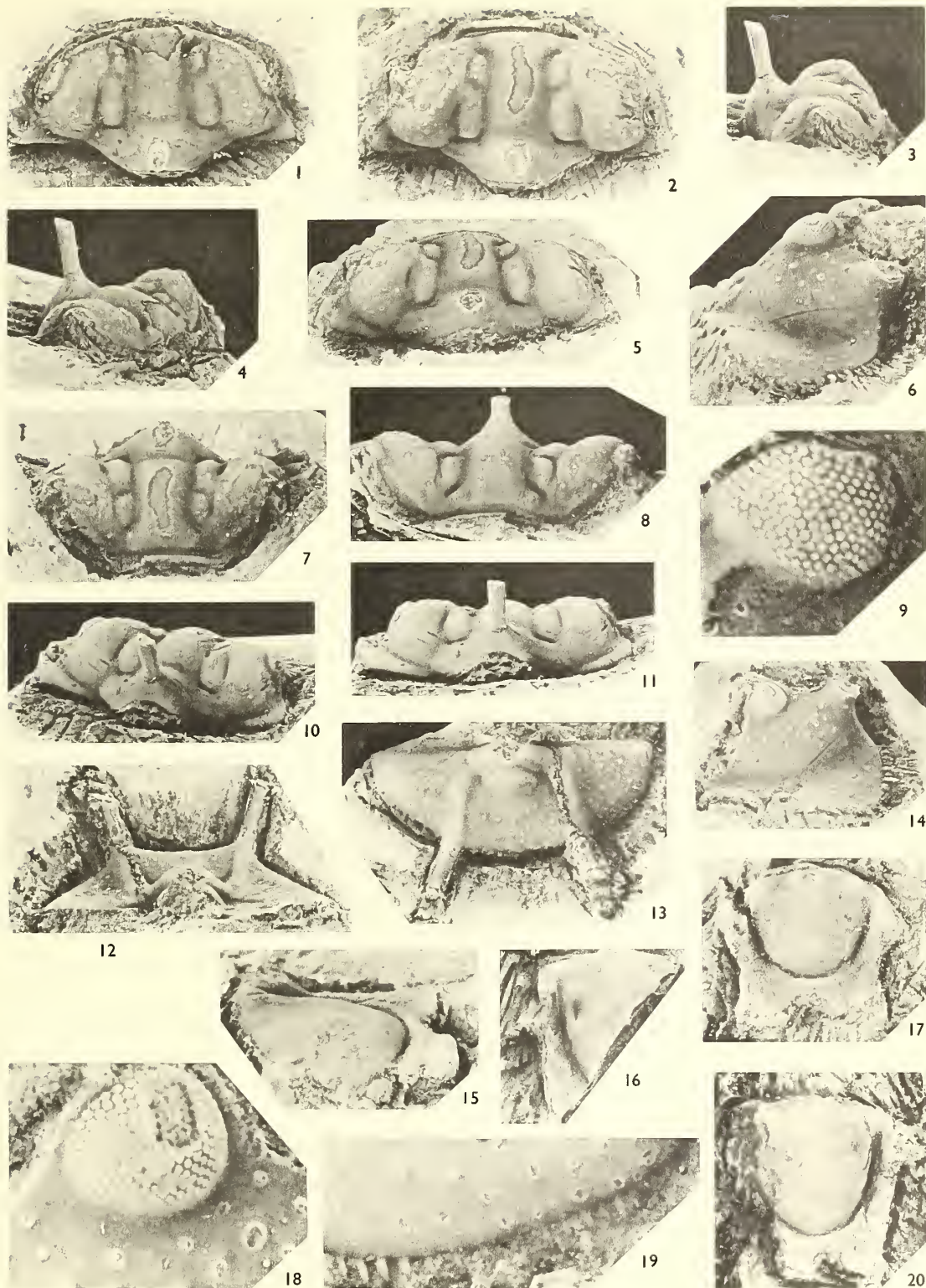
Material. In addition to the types, several cranidia, pygidia, one free cheek, and many thoracic segments.

Type locality and Horizon. The label accompanying the material reads, 'Menian Kalk (zone 9 mydlak), Zlatý Kůň; Professor Jahn 1904'. This information and the profile given by Jahn (1903, p. 21, fig. 4; see also Chlupáč, 1959, fig. 7, pp. 475–6), allows the material to be accurately placed in the Devonian succession exposed at Zlatý Kůň; the zone 9 corresponding to a local lens of soft limestone near the base of the *Acanthopyge* Limestone, i.e. at the base of the Upper Eifelian (Chlupáč, personal communication). The occurrence in the material of *Phacops* cf. *breviceps* also supports this conclusion.

Associated fauna listed by Chlupáč (1957, p. 473; 1959, pp. 490–5).

EXPLANATION OF PLATE 55

Figs. 1–20. *Isoprusia mydlakia* gen. et sp. nov., *Acanthopyge* Limestone (Upper Eifelian), Zlatý Kůň, Bohemia. 1, 3, 4, 10, 11, Mbg. 398, holotype, cranidium; dorsal, right lateral, oblique side, oblique posterior, and posterior views; $\times 4$. 2, 5, 7, dorsal view, posterior view showing posterior occipital band and anterior view of Mbg. 399, cranidium with exoskeleton partly exfoliated; $\times 4$. 8, Mbg. 400, slightly damaged cranidium with exoskeleton complete; anterior view; $\times 5$. 6, 14, 18, Mbg. 401, free cheek and eye lobe; 6, left lateral view; $\times 6$. 14, anterior view; $\times 4.5$. 18, external surface of eye lobe, oblique view; $\times 18$. 12, 13, anterior and dorsal views of Mbg. 402, pygidium; $\times 4$. 19, Mbg. 403, postero-lateral margin of pygidium showing secondary border spines; dorsal view; $\times 18$. 15, 20, oblique left lateral and dorsal views of Mbg. 404, internal mould of incomplete hypostoma; $\times 7.5$. 16, Mbg. 405, internal mould of incomplete hypostoma showing small depression on antero-lateral part of median body; dorsal view; $\times 6$. 17, Mbg. 406, small hypostoma, dorsal view; $\times 12$. 9, Mbg. 407, complete eye lobe, oblique lateral view; $\times 18$.



Description. Cranidium (Pl. 55, figs. 1, 2; Pl. 57, fig. 13) trapezoidal in outline, gently convex (sag., tr.). Glabella (Pl. 55, figs. 3, 8, 11), gently convex (sag., tr.) maximum width (tr.) at occipital ring tapering forward to slightly more than half this width at frontal lobe; length (sag.) approximately equal to maximum width. Occipital ring of length (sag.) slightly less than half total glabellar length, becoming narrower (exs.) where its lateral parts fuse with inner area of fixed cheek. Outline of posterior margin of ring strongly curved posteriorly; median part rather strongly convex (tr.) and bearing a slim occipital spine (length unknown), which arises from inside posterior margin (Pl. 55, figs. 3, 10, 11). Spine inclined backwards at approximately 70–80°. Occipital furrow broad, shallow and transverse medially, deepened as it becomes directed backwards and outwards around base of L_1 . Occipital lobes lacking. Posterior occipital band (Pl. 55, figs. 5, 10, 11) indistinctly separated from remainder of ring; widest and vertically sloping beneath base of spine, becoming slightly narrower and turned inwards and forwards laterally. Two pairs lateral glabellar lobes, L_1 the larger; both weakly convex and elongated (exs.). S_1 shallow, directed obliquely outwards and forwards, deepest between lobes becoming very shallow adjacent to dorsal furrow. S_2 shorter, very deep and slot-like (Pl. 57, fig. 13). Median lobe (Pl. 55, figs. 8, 11) gently convex (tr.) almost flat longitudinally (Pl. 55, fig. 3); frontal lobe sloping steeply downwards to anterior border furrow. Median lobe parallel-sided and separated from lateral lobes by broad, shallow longitudinal furrows which run into the curved S_2 furrow thus delimiting the broad lateral expansion of frontal lobe. Immediately in front of S_2 a small prominent swelling (Pl. 55, figs. 2, 8; Pl. 3, fig. 13), which may represent a third lateral lobe. Dorsal furrow deepest between adjacent parts of fixed cheek and lateral lobes, elsewhere, weakly defined and marked only by change in slope. Fixed cheek subtriangular, tapering forward from maximum width (tr.) just posterior to palpebral lobe; moderately to strongly convex (tr.), highest point on transverse line drawn midway through palpebral lobe. Such a line passes just posterior to outer extremity of S_1 furrow and crosses median glabellar lobe at approximately half length (sag.). When cranidium is viewed from anterior (Pl. 55, fig. 8), highest point of cheek above the level of median lobe. From highest point, cheek slopes gently forwards and then more steeply downwards to eye ridge; posteriorly cheek more steeply inclined and posterior part drops vertically down to posterior margin. Palpebral lobe gently curved and sloping slightly outwards from side of and below highest point of fixed cheek; lobe separated from cheek by broad shallow palpebral furrow which runs into shallower furrow along inner side of eye ridge (Pl. 55, fig. 1). Eye ridge broad, weakly defined, and directed forward before curving around outer anterior part of cheek to merge with smooth depressed area at lateral expansion of frontal lobe (Pl. 55, fig. 8). Anterior branch of facial suture curves forwards outside and sub-parallel to eye ridge and crosses anterior border (Pl. 55, fig. 8). Latter straight, gently arched (tr.) narrow (sag.) separated from frontal lobe by narrow, deep border furrow which becomes wider (exs.) and deepened just inside suture (Pl. 55, fig. 2). Posterior branch of suture continued outwards and downwards at some 45° to run out and over posterior margin. Posterior border furrow shallow to lacking at inner corner where fixed cheek and occipital ring fuse; laterally, furrow deepens and curves forwards around base of fixed cheek separating it from gently convex border widest (exs.) at the suture. Posterior margin (Pl. 55, fig. 11) gently swept upwards at suture, curved under with short downwardly projecting edge to doublure. External surface of cheeks,

fronto-median lobe, and lateral glabellar lobes covered with evenly, but widely spaced spine bases; furrows, occipital ring, and posterior border smooth.

Free cheek (Pl. 55, figs. 6, 14) wider (tr.) than long (exs.), with approximately straight anterior and sigmoidal lateral margins. Anterior border area near suture narrow and convex, becoming flatter and broader (exs.) laterally, here occupying half cheek length. A broad, smooth concave area separates lateral margin from convex part of cheek; area becoming deeper and narrower (exs.) near anterior suture. Librigenal spine arising from just inside border, its base merging with the lateral border and convex part of the cheek. Spine present on one specimen (Mbg. 407) but incomplete; apparently slim and directed straight upwards and backwards. One isolated spine curves distally at its tip. Lateral margin deep and ventrally directed immediately beneath librigenal spine (Pl. 55, fig. 6) becoming lower and rolled under towards fronto-lateral margin. At this point, six small, short peg-like border spines (Pl. 55, fig. 14), directed outwards and downwards from upper edge. Spines extend around outer lateral area as indicated by broken spine bases, but they do not extend along the whole length of anterior margin. Eye (Pl. 55, fig. 18) ovoid in plan, situated on highest point of cheek and sloping gently outwards and downwards; non-stalked and arising directly off cheek surface.

Eye surface (Pl. 55, fig. 9) covered in small, closely packed hexagonal lenses each facet convex externally. Convex part of cheek and flattened border with regularly spaced spine bases which extend on to and down the length of librigenal spine.

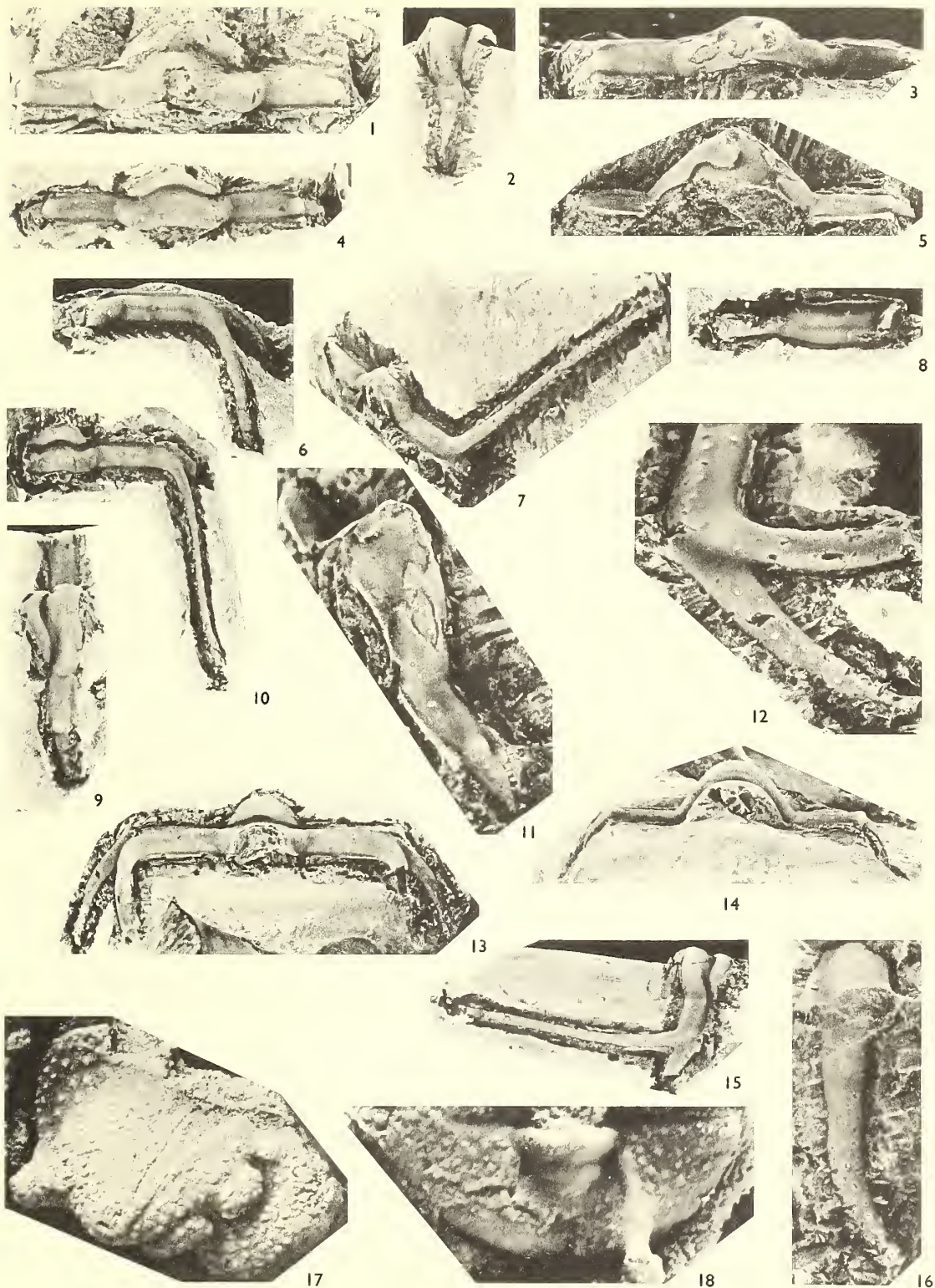
Hypostoma (Pl. 55, figs. 15–17, 20) subquadrate, slightly wider (tr.) than long (sag.). Anterior margin gently curved convex forwards; posterior margin with deep, narrow notch. Median body shield-shaped, gently convex (sag. and tr.), delimited by deep narrow border furrow which runs from antero-lateral margin convergently backwards to circumscribe posterior margin of body. Short dorsally directed anterior wings; lateral

EXPLANATION OF PLATE 56

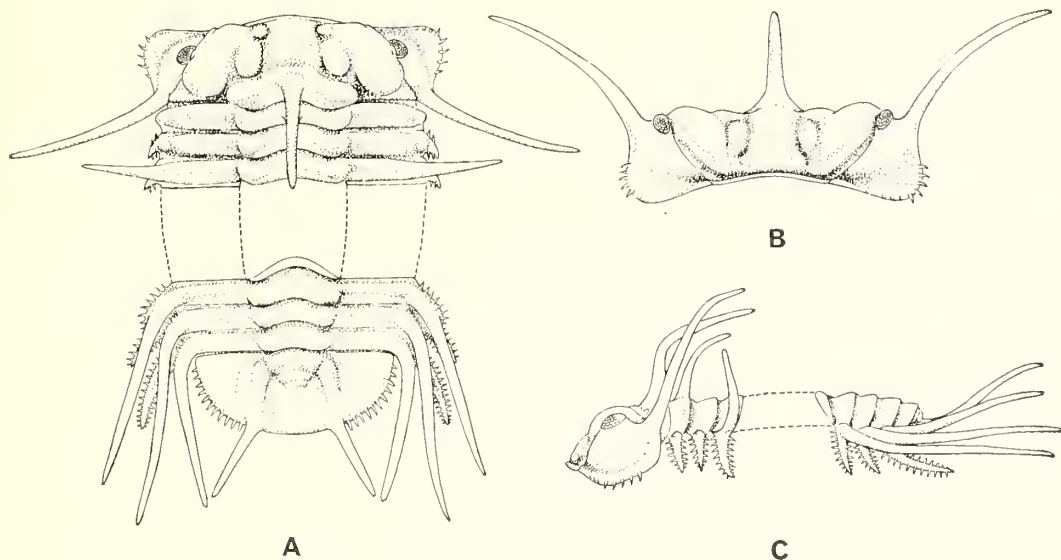
Figs. 1–16, *Isoprusia mydlakia* gen. et sp. nov. Thoracic segments; all specimens paratypes. 1, Mbg. 408, dorsal view of assumed first segment, showing broken base of median rachial spine, pleural area with faint furrow, and articulating flanges and sockets; $\times 5$. 3, 5, 11, Mbg. 409; first thoracic segment; 3, 5, dorsal and anterior views; $\times 6$. 11, oblique left lateral view showing articulating flanges, tubercle-like pleural spine and short barbed terminal spine; $\times 9$. 2, 4, 9, 14, lateral, dorsal, oblique lateral and anterior views of Mbg. 410; ? second thoracic segment; note absence of median rachial spine, unfurrowed pleural area, tubercle-like pleural spine and short, downwardly directed terminal spine; $\times 4$. 8, Mbg. 411; dorsal view of incomplete segment with upwardly directed pleural spine; note well-developed pleural furrow; $\times 4$. 6, Mbg. 412; dorsal view of more posterior segment with lengthened pleural spine curved backwards; note longer and curved terminal spine, also pleural furrow; $\times 4$. 7, Mbg. 413; similar segment; oblique lateral view; $\times 4$. 10, 15 Mbg. 414; dorsal and right lateral view of incomplete posterior segment; $\times 4$. 12, 13, Mbg. 415; assumed tenth thoracic segment 13, dorsal view; $\times 4$. 12, left lateral view of distal end showing the blade-like pleural spine and the long, backwardly curved, barbed terminal spine; note also articulating flanges and presence of articulating process only; $\times 9$. 16, Mbg. 416; left lateral view of long terminal spine of a posterior segment; $\times 9$.

Fig. 17, *Isoprusia sandbergeri* (R. and E. Richter), Stringocephalus Limestone (Lower Givetian), Villmar-Lahn, West Germany. Dorsal view of holotype (Nat. Hist. Museum, Wiesbaden); $\times 10$. The incomplete cranium, an internal mould, has been compressed from the left-hand side along the line of the longitudinal furrow so that the glabella has become partly pushed under.

Fig. 18, *Isoprusia cornuticauda* (Erben), Greifensteiner Kalk (Eifelian), Wiege near Greifenstein, Harz, West Germany. Dorsal view of holotype T.U. Ar. 1010/40, a pygidium with damaged left pleural region; $\times 10$.



margin convex and narrow anteriorly with small pointed shoulder and shallow lateral notch. Posteriorly, margin becoming wider, outwardly sloping and produced into flattened ear-like projections separated by the posterior notch. Latter does not reach border furrow. On largest hypostoma (Pl. 55, fig. 16) a short ovoid depression occurs on edge of median body opposite shoulder. Depression absent on the smallest specimen



TEXT-FIG. 1. *Isoprusia mydlakia* gen. et sp. nov. Reconstruction. A, dorsal view; B, anterior view of cephalon; C, left lateral view. Number of thoracic segments unknown. Approximately $\times 2$.

(Pl. 55, fig. 17), slightly impressed on the next largest one (Pl. 55, fig. 20). Median body smooth to slightly granulated; lateral margin and posterior ears very finely granulated.

Number of thoracic segments not known but the reconstruction (text-fig. 1) has been made assuming the number to have been ten. From the attitude of the pleural spines, it has been assumed that those segments which have spines directed laterally outwards or upwards and forwards belong anteriorly, and those on which the spines are directed progressively more backwards, belong posteriorly. Such an assumption seems a valid one since this is always the case in the Miraspidinae and Apianurinae Whittington (1956a), two subfamilies with genera possessing similarly shaped thoracic pleurae. Numerous fairly complete and some broken segments allow the following descriptions and observations to be made. Rachis (Pl. 56, figs. 1, 2, 5, 14) moderately to strongly convex and wide (tr.) occupying almost half entire width of segment. Posterior margin gently curved convex forward (sag.); articulating halfring approximately half as long (sag.) as rachial ring; anterior margin convex forward like articulating furrow, sloping backwards and becoming narrower at dorsal furrow. Pleurae horizontal and flattened; anterior segments (Pl. 56, figs. 1, 3, 4) smooth or very weakly furrowed; posterior segments (Pl. 56, figs. 6-8, 10, 13) with shallow but obvious pleural furrow. Anterior and posterior margins straight with very narrow (exs.) flattened flanges. Small fulcral

articulating (anterior) and socket (posterior) processes developed (Pl. 56, figs. 3, 11, 16). Principal pleural spine on at least the first two anterior segments in the form of a small upwardly and outwardly directed tubercle (Pl. 56, figs. 1–5, 9, 11, 14) from the pleural surface. Immediately beneath tubercle (Pl. 56, figs. 2, 9, 11), short, tapering terminal spine. Latter downwardly directed, flattened dorso-ventrally and bearing row of small spines along edges. Two pleural segments (Pl. 56, figs. 1, 3, 5, 11) with a similar pleural spine, have a rachis like the occipital ring of the cranidium including the median spine (unfortunately this was broken during preparation, but the base can be seen). In these segments, the rachis is slightly greater than twice the width (tr.) of the very short pleural area and such proportions fit those of the occipital ring and posterior margin of the larger cranidia. For these reasons, it is thought most likely that this type of segment is the first. Segments (Pl. 56, figs. 6–8, 10, 13, 15) from positions more posterior have a rachis of the same configuration as those described for pleurae without median rachial spine but in addition, the tubercle-like pleural spine is produced into long, slim pleural spines, the lengths, curvature, and directions of which are indicated on the reconstruction. Articulating flanges and processes visible on pleurae with upwardly directed pleural spine (Pl. 56, fig. 8) while only flanges and anterior process visible on segments in which pleural spine is directed backwards (Pl. 56, figs. 7, 10, 15). Terminal spines as on anterior pleurae but much longer (Pl. 56, fig. 16) and curved backwards distally. Pleural spines circular in cross section. Pleurae of type shown (Pl. 56, fig. 13) regarded as representing the tenth segment. Pleural area, rachis, and halfring identical to other posterior segments, but pleural and terminal spine (Pl. 56, fig. 12) differ in, (1) pleural spine flattened in cross-section and blade-like; spine produced backwards and slightly upwards from fulcrum, becoming incurved distally; (2) terminal spine similar to those on other segments, but inclined backwards and almost horizontal.

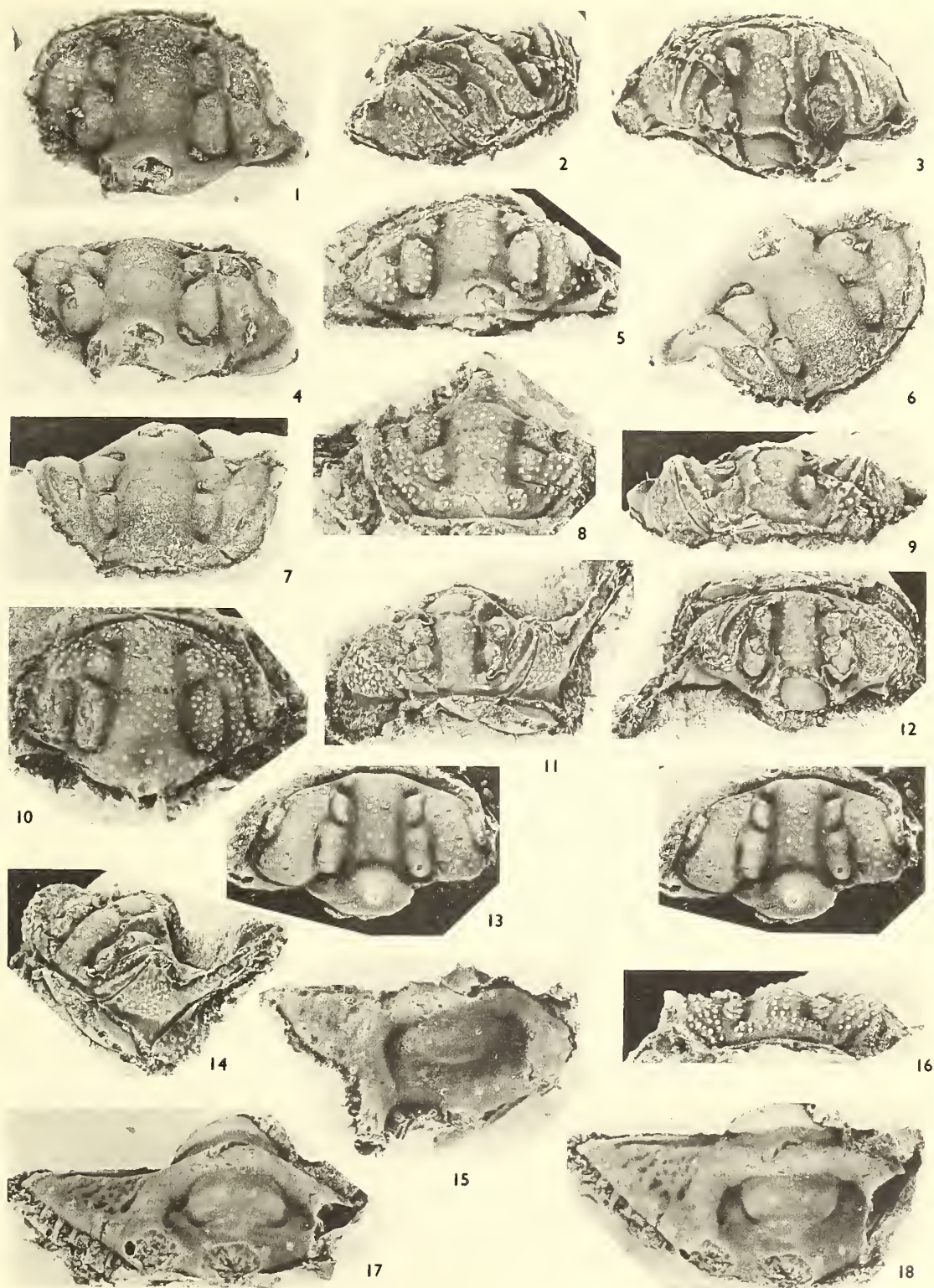
On all segments, pleural area smooth or with odd spine bases; rachis with transverse row of small spine bases which extend diagonally down the lateral parts. Terminal and pleural spines apparently finely spined.

EXPLANATION OF PLATE 57

Figs. 1, 4, 6, 7. *Isoprusia laportei* (Hawle and Corda), ? Suchomasty Limestones (Upper Emsian–Lower Eifelian), Měňany near Koněprusy, Bohemia. Plaster cast of lectotype, N.M.P. ČF639; cranidium, part internal mould; 1, 6, dorsal and oblique views; 4, posterior view showing posterior occipital band; 7, anterior view; $\times 3$.

Figs. 2, 3, 5, 8–12, 14, 16. *Isoprusia ursula* (Barrande), Upper Koněprusy Limestone, Koněprusy area, Bohemia. 2, 3, 9, plaster cast of holotype, N.M.P. ČF635, incomplete cephalon, internal mould; 2, 3, oblique and dorsal views showing posterior position of eye and long anterior facial suture; 9, anterior view; $\times 3$. 5, 16, M.C.Z. 4215, incomplete cranidium; 5, posterior view showing narrow posterior occipital band; 16, anterior view; $\times 6$. 8, 10, M.C.Z. 4216, incomplete cranidium, anterior and dorsal view showing narrow (sag.) occipital ring and backwardly directed spine; $\times 4$. 11, 12, 14, M.C.Z. 4217, incomplete and partly exfoliated cephalon, anterior, dorsal, and oblique views showing position of free cheek and librigenal spine; $\times 3$. Scharý Collection.

Fig. 13. *Isoprusia mydlakia* gen. et sp. nov. Mbg. 400, incomplete cranidium, dorsal stereograph; $\times 4$. Figs. 15, 17, 18. ? *Koneprusia subterarmata* (Barrande), Suchomasty Limestones (Upper Emsian–Lower Eifelian), Měňany near Koněprusy, Bohemia. 17, 18, plaster cast of lectotype N.M.P. ČF644a, incomplete pygidium, internal mould; 18, dorsal view; 19, posterior view; $\times 5$. 15, plaster cast of paralectotype, N.M.P. ČF664b, incomplete pygidium, internal mould, dorsal view; $\times 5$.



BRUTON, Devonian odontopleurid trilobites

Discussion of Pleural Modification

Accepting the theory that during ontogeny new segments are formed by growth to the anterior border of the hind-most somite and then released forward (Stubblefield 1926), it follows that the most anterior segments are the first formed, and the posterior, the last. Thus it is possible that the posterior segments resemble in character more closely the original pleural condition, the anterior showing some modification. In *Isoprusia mydlakia*, the anterior segments either lack the pleural furrow or have it very faintly defined, while on the posterior segments it is still obviously present. On segments with an upwardly directed spine (Pl. 56, fig. 8), a pleural furrow with point of origin at the antero-lateral part of the rachis, is directed straight outwards towards the base of the spine where it becomes obliterated. Thus the pleura is divided into two bands of equal length (sag.), the spine base straddling both bands. In more posterior segments (Pl. 56, figs. 6, 10, 13), a pleural furrow runs diagonally across the pleural area and distally follows the inner posterior part of the pleural spine base. Hence the pleura is divided into two bands as before, but here the principal pleural and terminal spine both belong to the anterior band. The degree of modification is taken further in the most anterior segments (Pl. 56, figs. 1, 2, 4, 9) where the terminal spine is a downward continuation of the full pleural width, and the pleural spine is reduced to a small tubercle. Transverse sections of the segments suggest that the doublure does not extend beneath the pleura, and only the curled-down edge of the pleura forms the articulating process and socket. Such an arrangement is similar to that found in *Ceratocephala laciniata* Whittington and Evitt (1954, p. 59, pl. 6, figs. 5, 6). It seems reasonable to suppose that on the anterior segments, the reduction to a tubercle of the pleural spine, is an accommodation to ease of articulation and possibly enrolment, since an upwardly directed spine would interfere with the librigenal spine. In view of the obvious presence of a pleural furrow on the posterior segments, it seems unlikely that the anterior segments represent the original pleural type from which the posterior segments have become secondarily modified by the extreme elongation of the tubercle in the form of a spine.

To homologize the pleural spines in *Isoprusia* with those found on the pleurae of other odontopleurid genera is more difficult. In genera (*Primaspis*, *Diacanthaspis*, *Leonaspis*, and others; see Whittington 1956a) with a recognizable pleural furrow, the principal pleural spine, without exception, belongs to the posterior band, and a second spine, if developed, to the anterior band. Even in *Ceratocephala laciniata* Whittington and Evitt, the second spine (= barbed spine), belongs to the posterior part of the segment. In *Isoprusia*, it forms as a continuation of the full pleural width, or belongs to the anterior band. For this reason I have called this spine in *Isoprusia mydlakia* terminal (not terminal in the sense of Reed 1925; Prantl and Přibyl 1949; = anterior spine of Whittington 1956a, p. 161). It has been shown that the pleural spines can belong to either band and thus it is difficult to use them for comparative morphology.

Isoprusia laportei (Hawle and Corda, 1847)

Plate 57, figs. 1, 4, 6-7

1847 *Odontopleura Laportii* Hawle and Corda, p. 156.

1852 *Acidaspis Laportei*: Barrande, p. 750, pl. 39, fig. 22 only.

1926 *Acidaspis* (*Leonapis*) *laportei*: Kegel, p. 20, pl. 2, fig. 15.

- 1949 *Acanthaloma* (*Acanthaloma*) *laportei*: Prantl and Přibyl, p. 162, pl. 3, fig. 3 only.
1950 *Ceratocephalo* (*Leonaspis*) *laportei*: Erben, p. 281.
1952a *Acanthaloma* (*Acanthaloma*) *laportei*: Erben, p. 289, pl. 20, figs. 11–12.
1965 *Koneprusia laportei laportei*: Lütke, p. 223, pl. 22, figs. 9–11; text-fig. 35a; not *Koneprusia laportei* n. subsp. A.
non 1957 *Leonaspis* (*Leonaspis*) *laportei*: Osmólska, p. 69, pl. 3, fig. 8.

Lectotype (Prantl and Přibyl 1949, p. 162). N.M.P. ČF639, Plate 57, figs. 1, 4, 6–7, Cranidium in limestone and still retaining part of exoskeleton.

Material. Several paralectotypes, N.M.P. ČF640; the specimen of Kegel, H.U. T292; the original cranidia of Erben, H.U. T343–4; plus topotype material from the Scharý Collection. M.C.Z. 4213–14.

Locality. Měňany near Koněprusy, Bohemia.

Horizon. Not known with certainty, but most probably from the Suchomasty Limestones (Upper Emsian–Lower Eifelian).

Description. The species *Isoprusia laportei* (Pl. 57, fig. 1), is closest to *I. mydlakia* (Pl. 57, fig. 13), but differs in the following features: (1) More strongly inflated fronto-medial glabellar lobe and lateral lobes. (2) The less strongly inflated fixed cheek which is flatter and narrower (tr.) and slopes less steeply down to the posterior margin (Pl. 57, figs. 6, 7). (3) Highest part of cheek and that of median lobe at approximately the same level (Pl. 57, fig. 7), when specimen is viewed from the anterior. In this respect *I. laportei* resembles *I. ursula* (Pl. 57, fig. 9), but in this species the position of the eyes (Pl. 57, figs. 3, 10) and the configuration of occipital ring and posterior band (Pl. 57, figs. 5, 10) are different. In *I. mydlakia* (Pl. 55, fig. 8), the median glabellar lobe is lower than the adjacent fixed cheeks. The hypostoma which Lütke (1965, pl. 22, fig. 10) figured as belonging to *laportei*, differs from that of *I. mydlakia* in having a narrower posterior notch and deeper middle furrows. The free cheek, thorax, and pygidium of *I. laportei* are not known.

Discussion. New collections made by Barrande (1852, p. 751, pl. 39, fig. 25) enabled amplification of the original description, and the description of a pygidium considered to belong to the species. Prantl and Přibyl (1949, pl. 3, fig. 4) also thought that the pygidium belonged to the species, but it is quite unlike any known for the genus *Isoprusia* and is more likely to belong to a species of *Leonaspis*. Vaněk (1961, p. 85, footnote) has noted the similarity to *Leonaspis pigra* (Barrande, 1872).

Prantl and Přibyl (1949, p. 162) assigned this species to *Acanthaloma* (= *Leonaspis*). In their remarks, they noted that the specimen figured by Barrande does not show distinctly 'The subtrigonal areas on both sides of the frontal lobe, nor the course of the anterior branch of the facial suture, which deviates distinctly from the ocular ridge'. Study of the type (Pl. 57, figs. 1, 6, 7) does not confirm this observation. The anterior suture is curved convergently towards the anterior border and runs sub-parallel and just outside the weakly defined eye ridge. In other respects, the glabella, frontal lobe with lateral swellings, and shape of occipital rings are like those of the other species now placed in the genus *Isoprusia*. Examination of the second cranidium figured by Prantl and Přibyl (1949, pl. 10, fig. 9), leads me to believe that this belongs to the genus *Leonaspis*.

Horizon. The exact horizon in which the lectotype was found is still not known, and it seems likely that Prantl and Přibyl were wrong in referring all of the reddish limestone material from Měňany to the Vinařice Limestone. At Měňany, beds from the lowest Pragian to Upper Eifelian are exposed in which the lithologies are very much alike, but careful collecting has shown the distinctiveness of faunas from the Vinařice, Suchomasty, and Acanthopyge Limestones (see Chlupáč and Vaněk 1957; Chlupáč 1959).

The specimen of Kegal from the Steinberger Kalk of Lindener Mark is exceedingly small, but it is like those figured by Erben (1952a) and Lütke (1965, pl. 22, figs. 9, 11) from the Upper Emsian of the Harz, and all seem to be indistinguishable from the Bohemian material of *I. laportei* (for remarks cf. Lütke 1965, pp. 223–4).

Isoprusia ursula (Barrande, 1872)

Plate 57, figs. 2, 3, 5, 8–12, 14, 16

1872 *Acidaspis ursula* Barrande, p. 84, pl. 16, fig. 28.

1949 *Koněprusia ursula*: Prantl and Přibyl, p. 201, pl. 3, fig. 25.

1957 *Leonaspis* (L) *laportei*: Osmólska, p. 69, fig. 4; pl. 3, fig. 8.

Holotype. N.M.P. ČF635, Pl. 57, figs. 2–3, 9. An incomplete cephalon with damaged occipital ring and fronto-median lobe as internal mould.

Material. In addition to the type, two cranidia and an incomplete cephalon from the Schary Collection, M.C.Z. 4215–17.

Locality and Horizon. The type specimen was collected from the general area of Koněprusy, most probably from the Upper Koněprusy Limestones.

Description. Cranidium (Pl. 57, figs. 9, 11, 16) flat to gently convex (tr.); when specimen is viewed from anterior, highest point of median glabellar lobe and fixed cheeks at approximately the same level. Median glabellar lobe widest at occipital furrow, tapering forwards (Pl. 57, figs. 10, 12); dorsal furrow shallow. Lateral lobes suboval, and inflated to same level as adjacent cheek. Occipital ring (Pl. 57, figs. 5, 10) broad (tr.) very short (sag.) and gently convex. Occipital furrow shallow and only change of slope marks off ring from median lobe. Narrow posterior band (Pl. 57, fig. 5) separated from lateral part of anterior band by shallow furrow; medially, furrow shallow to lacking and separation of two bands indistinct. Ring with stout spine which curves backwards in almost horizontal plane from posterior margin. Eye ridge narrow (tr.) and disposed on highest outer part of fixed cheek. Latter very narrow (tr.). Palpebral lobe far back and directed upwards and slightly backwards (Pl. 57, figs. 5, 16), so that mid-point lies on transverse line through middle of L_1 . Anterior facial suture very long (exs.), runs straight forward to point opposite outer end of S_1 furrow, and then curves inwards to anterior margin parallel to and outside eye ridge (Pl. 57, figs. 2, 9, 14). Posterior suture (Pl. 57, fig. 12) at approximate right-angle to anterior suture at base of eye; from here, directed outwards and downwards across cheek to border furrow before curving around base of librigenal spine.

Free cheek as in *I. mydlakia*, but more convex and swollen around eye. On the holotype (Pl. 57, fig. 3) only this part of the cheek is visible, the lateral margins being obscured by matrix. The material from the Schary Collection at Harvard (Pl. 57, figs. 11, 14) shows the sigmoidal outline and the lateral margin with at least five short fringing spines. Librigenal spine directed upwards and backwards.

Fronto-median glabellar lobe with sub-symmetrical rows (both tr. and exs.), of coarse

granules or spine bases. Remainder of cephalon with granules or spine bases more unevenly distributed.

Thorax, pygidium, and hypostoma not known.

Discussion. The species resembles *Isoprusia laportei*, but the narrow fixed cheeks, eye position, shape of occipital ring, and nature of posterior band and spine in *I. ursula* are distinguishing features.

Osmólska (1957) noted that the glabellar proportions of the Couvinian specimens from the Holy Cross Mountain area of Poland were different to those specimens from Bohemia and Germany. Dr. Osmólska has kindly supplied additional photographs of her material and study of these suggests a closer relationship to *I. ursula* than *I. laportei*, on account of the transverse profile and shape of occipital ring and spine. She notes (p. 70) that the eye ridge and palpebral lobe is not discernible on the material, but study of her figure (pl. 3, fig. 8) clearly shows a well-defined eye ridge and base of the palpebral lobe; the latter positioned far back. The Polish material comes from a higher horizon than Barrande's type, but Osmólska (1957, p. 54) has shown that some of the species associated with the Polish Couvinian fauna are known from the Lower Devonian of both Bohemia and the Harz regions.

During a recent visit to the Central Geological Museum at Leningrad, I had the opportunity of examining the specimen described from the Middle Devonian of Kazakhstan (Turkestan) by Weber (1932, p. 134, pl. 1, fig. 20a-c) as *Acidaspis cornuta*. I have no doubt that this is a species of *Isoprusia* which is closely related to *I. ursula*.

Acidaspis cornuta Weber 1932 is a junior primary homonym of *Acidaspis cornuta* Beyrich 1846, a species of *Miraspis* from the Upper Ordovician of Sweden. However, I do not intend to designate a new name here, but leave this until the specimen is redescribed by one of my Russian colleagues.

Isoprusia cornuticauda (Erben, 1952)

Plate 56, fig. 18

1952a *Orphanaspis cornuticauda* Erben, p. 314, pl. 20, fig. 13.

Holotype. T.U. Ar.1010/40, Plate 56, fig. 18. Incomplete pygidium.

Locality. 'Wiede' near Greifenstein, Harz, West Germany.

Horizon. Greifensteiner Kalk (Eifelian).

For full description, see Erben (1952a).

Discussion. The similarity between this species and the pygidium of *I. mydlakia*, indicates that *cornuticauda* should be transferred to the genus *Isoprusia*.

This specimen of *cornuticauda* is very similar to the pygidium described and figured by Lütke (1965, p. 226, text-fig. 36c) under the name *pennata*. Further material may prove that there is no distinction. These pygidia differ from *I. mydlakia* in not having the numerous secondary border spines. The cranidium of *I. pennata* and *I. mydlakia* are quite distinct.

It should be pointed out that the free cheek of *I. pennata* has been reconstructed by Lütke (op. cit., p. 226, text-fig. 36a) from broken material (cf. Lütke, pl. 22, fig. 13a, b), and I am not satisfied that the reconstructed outline is reliable. A free cheek with

a sigmoidal outline like that of *I. mydlakia* (Pl. 55, figs, 6, 14) and *I. ursula* (Pl. 57, fig. 14) is more likely to be the correct one.

Isoprusia sandbergeri (R. and E. Richter, 1917)

Plate 56, fig. 17

1850 '*Odontopleura fragmenta, speciei incertae* (? novae)' G. and F. Sandberger, p. 56, pl. 2, fig. 5a, b.

1917 *Acidaspis* (*Ceratocephala* ?) *sandbergeri* R. and E. Richter, p. 467, fig. 8a, b.

Holotype. Plate 56, fig. 17. Incomplete and distorted cephalon. Type deposited in the Natural History Museum, Wiesbaden, West Germany.

Locality. Villmar-Lahn, West Germany.

Horizon. Stringocephalus Limestone (Lower Givetian).

Description. Despite the compression and distortion, the free cheek and eye lobe (Pl. 56, fig. 17) does not appear to have been displaced to any great extent (cf. R. and E. Richter 1917, p. 467).

The posterior position of the eye and the long, gently curved eye ridge, is reminiscent of *Isoprusia ursula*. The free cheek, although damaged along the anterior margin is more like that of *I. mydlakia*, in so far as the cheek area is less convex than in *I. ursula*. The lateral swelling of the frontal glabellar lobe is typical of the genus *Isoprusia*. The convexity and outline of the glabella and lobes, and the depths of furrows have no doubt been exaggerated owing to the distortion of the specimen.

Discussion. R. and E. Richter, assigned this species with some reservation to *Ceratocephala*, and remarked on the unusually high stratigraphic position of the genus. *Isoprusia sandbergeri* is, to date, the youngest known for the genus, and one of the youngest species of the family Odontopleuridae Burmeister.

? *Isoprusia sperata* (Barrande, 1872)

1872 *Acidaspis sperata* Barrande, p. 423, pl. 32, figs. 20–21.

1872 *Acidaspis sparsa* Barrande, p. 82.

1949 *Koněprusia* (?) *sperata*; Prantl and Přibyl, p. 202.

Discussion. The type of *Acidaspis sperata* illustrated by Barrande is extremely misleading and inaccurate when one compares the figure and actual specimen, a poorly preserved internal mould of a pygidium. The rachis seems to have three rings; the small median outgrowth at the posterior margin and the small secondary border spines are just discernible (it is impossible to count the actual number; cf. Prantl and Přibyl 1949, p. 202). In addition, details of the pleural region, ornamentation and general outline are not apparent. The holotype is the only known specimen and its preservation makes it an inadequate basis for the species.

Barrande (1872, p. 424) gave the locality of Braník which most likely refers to the former 'Podolská cementárna' (= cement works). Only the lowermost Dvorce–Prokop Limestone (Pragian) is exposed at this locality (Chlupáč, personal communication).

Barrande described both *Acidaspis sperata* and *A. sparsa* from the same locality and horizon, and their respective descriptions seem remarkably similar. Further confusion is caused by the fact that both species were said to be figured (Barrande 1872, pl. 32), but only the figure of *Acidaspis sperata* appears on this plate. To my knowledge, no specimens labelled *A. sparsa* have been found amongst the Barrande collections at the National Museum, Prague.

Vaněk (1961, p. 85) notes that former references to the occurrence of *laportei* (presumably of cranidia) from the Dvorce-Prokop Limestone, should in fact relate to *sperata*, but this cannot be proved with the material available.

Genus KONEPRUSIA Prantl and Příbyl 1949

Type species (by monotypy). *Acidaspis fuscina* Novák 1883 (not traced).

Diagnosis. Pygidium differing from that of *Isoprusia* gen. nov., in being more triangular with the development of a stout median border spine. In the type species, the remainder of the border is apparently smooth, but one species tentatively assigned to this genus shows the development of numerous small secondary border spines. Details of thorax and cephalon not known.

Discussion. In erecting the genus *Koneprusia*, Prantl and Příbyl (1949, pl. 3, fig. 26; pl. 5, fig. 2) reproduced Novák's (1883, pl. 10, fig. 19a) two figures of the type species, an incomplete thorax and pygidium with very damaged cephalon attached. The type specimen was not rephotographed nor was any documentary evidence published of additional material. During my stay in Prague (Autumn, 1962) I was unable to trace the holotype among the collections in the National Museum and both previous and subsequent searches have also failed (Vaněk, personal communication, 9 March 1964). The type species of *Koneprusia* is thus only known from Novák's (1883, pl. 10, fig. 19a) illustration.

I have regarded the type of pygidium Novák portrays, with a well-developed stout median border spine, as sufficiently distinct to enable the separation of *Koneprusia* from *Isoprusia*. The species *K. fuscina* (Novák) is very rare and the pygidium has not been found during recent collections made by Dr. Chlupáč and Mr. Vaněk from the Acanthopyge Limestone. Thus, until an exoskeleton bearing the characteristic pygidium figured by Novák for *Acidaspis fuscina* is known, it is not possible to define the characters of thorax and cephalon in *Koneprusia*.

The description of the horizon and associated fauna listed by Novák (1883, p. 38; Prantl and Příbyl 1949, p. 200) would seem to indicate that the type species of *Koneprusia*, like that of *Isoprusia*, was collected from the Acanthopyge Limestone near Koněprusy. Mr. Vaněk (personal communication) has recently collected two incomplete cranidia from this horizon (I have seen casts of both specimens which have the strongly inflated fixed cheek characteristic of *Isoprusia mydlakia*) which he considers to be topotype material of *Koneprusia fuscina*. This cannot be proved because of the loss of the holotype of this species and the inadequate illustration of it given by Novák. For the same reasons, *K. fuscina* cannot be compared with the cranidium of *Isoprusia mydlakia*, but as outlined above, the pygidia are considered to be generically different.

? *Koneprusia subterarmata* (Barrande, 1846)

Plate 57, figs. 15, 17–18

- 1846 *Odontopleura subterarmata* Barrande, p. 18.
1847 *Odontopleura impar* Hawle and Corda, p. 157.
1852 *Acidaspis subterarmata*: Barrande, p. 749, pl. 39, figs. 16–17.
1949 *Koněprusia subterarmata*: Prantl and Přibyl, p. 200, pl. 3, figs. 27.
1961 *Koněprusia subterarmata*: Vaněk, p. 85 (footnote).
1965 *Koneprusia subterarmata*: Lütke, p. 222, text-fig. 34.

Lectotype (wrongly designated as holotype by Prantl and Přibyl), N.M.P. ČF644a, Pl. 57, figs. 17–18, one of Barrande's two syntypes. An incomplete pygidium; internal mould.

Paralectotype. N.M.P. ČF644b, Plate 57, fig. 15. Pygidium, internal mould.

Horizon. Not known with certainty, but most likely from the Suchomasty Limestone.

Locality. Měňany near Koněprusy, Bohemia.

Description. Pygidium (Pl. 57, figs. 15, 17–18), triangular, approximately three times as wide (tr.) as long (sag.). Rachis of two obvious rings and a low, very narrow (sag.) terminal portion marked off by weakly impressed transverse furrow. First ring broad (tr.) moderately convex; second ring lower and narrower (sag.); rachis not reaching posterior border. Articulating half ring as wide as first ring, very narrow (sag.); articulating furrow broad and shallow, curved forward medially. Dorsal furrow shallow along-side first ring, deepened around second, but becoming shallow and lacking posteriorly. Pleural ridge broad, weakly convex, runs outwards and curves backwards to be produced into stout, slightly outwardly and upwardly directed major border spine (length unknown). Stout median border spine (Pl. 57, fig. 15), directed from posterior margin; spine apparently of equal strength to major border spine. Secondary border spine bases visible beneath the major border spines and at least eight short, downwardly directed secondary spines (Pl. 57, figs. 17–18) from lateral margin. Pleural area flat to gently depressed between rolled lateral, and straight and flattened anterior margin. At least four prominent spine bases along lateral margin and a pair each side of median spine. Rachis with pair of spine bases on each ring.

Discussion. This species is tentatively assigned to *Koneprusia* on account of the triangular outline of the pygidium and the presence of the stout median border spine.

Both Barrande and Hawle and Corda collected their material from the general area of Měňany, but the exact stratigraphic horizon remains uncertain. Prantl and Přibyl (1949, p. 120) recorded the species as having come from the Vinařice Limestone (Pragian), but since then revision of the stratigraphy indicates that it may well have come from the Suchomasty Limestone (Upper Emsian–Lower Eifelian). To date, the remainder of the exoskeleton of this species is unknown.

ORIGINS AND RELATIONS OF *ISOPRUSIA*

The relationship of *Isoprusia* to other members of the Miraspidinae R. and E. Richter, 1917; emend. Whittington 1956a (= Ceratocephalidae of Prantl and Přibyl 1949; Erben 1952b) is still obscure, but certain exoskeletal features found in *Isoprusia* also

occur in *Dicranurus* (Lower-Middle Devonian), *Ceratocephala* (Llanvirn-Lower Middle Devonian; see Whittington 1963, p. 103, pl. 31, figs. 18, 21; pl. 32, figs. 1-3; Prantl and Přibyl 1949, p. 183), and *Miraspis* (?Arenig-Llanvirn-Lower Devonian; see Whittington and Bohlin 1958; Whittington 1956b, p. 515, pl. 60, figs. 1, 4).

Dicranurus (see Whittington 1956a, p. 248, text-fig. 18), like *Isoprusia*, has a cranidium which is trapezoidal in outline and the frontal glabellar lobe is expanded laterally. The eye position and sutural directions are also alike, but *Dicranurus* has a conical eye raised well off the cheek surface. The lengthened (sag.) and less convex (tr.) occipital ring of *Dicranurus* is an important difference, although the configuration of the occipital spines (paired and strongly curved in *Dicranurus*) is not considered of great taxonomic importance. The pleural regions of *Dicranurus*, with well-marked pleural furrow and ridge, points to a closer connexion with *Miraspis*, while the smooth or weakly furrowed pleural band of *Isoprusia* resembles those found in *Ceratocephala*. The hypostoma of *Isoprusia*, although having the shoulder and lateral notch (a family characteristic, Whittington 1956a, p. 170), has a deep posterior median notch and posterolateral ears quite unlike any odontopleurid hypostomata previously known. A shallow, median notch is found in both *Miraspis* (see Barrande 1852, pl. 39, fig. 8) and *Ceratocephala* (see Whittington 1956a, pl. 14, fig. 11; pl. 15, fig. 23) and may indicate a relationship. The pygidium of *Isoprusia* bears no resemblance to those known for *Ceratocephala* (see Barrande 1852, pl. 38, figs. 5, 18; Whittington and Evitt 1954, pl. 6, fig. 8), and its semicircular outline sets it aside from the subtrigonal shape of *Dicranurus*. The development or loss of secondary border spines or median spine, and the disposition of the pleural ridge in pygidia of *Isoprusia* suggests a modification of a *Miraspis*-like pygidium. The shortened (sag.) rachis is a characteristic of *Miraspis*.

The discovery of a *Miraspis* species in the early Ordovician of Sweden (Whittington and Bohlin 1958, p. 42, pl. 3, figs. 1-4) now shows that at this time, *Miraspis* was distinct from *Ceratocephala* (cf. Whittington 1956a, pp. 188-90, fig. 3). However, the fact that *Isoprusia* has features of the exoskeleton which are shared by both *Miraspis* and *Ceratocephala* indicates that this genus must be either derived from one or other of these stocks, or be derived independently from an unknown Cambrian root stock which also gave rise to *Miraspis* and *Ceratocephala*.

A similar origin for *Dicranurus* seems likely, but whether this genus lies on the same branch which gave rise to *Isoprusia* is not known.

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UNUSUAL STRICKLANDIID BRACHIOPODS FROM THE UPPER LLANDOVERY BEDS NEAR PRESTEIGNE, RADNORSHIRE

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ABSTRACT. Both smooth and strongly ribbed stricklandiid brachiopods occur together in early Upper Llandovery beds (C_1 – C_3) at Presteigne. *Aenigmastricklandia contorta* gen. et sp. nov. is proposed for the ribbed species, while the smooth species is assigned to *Stricklandia lens* aff. *progressa* Williams. *Aenigmastricklandia* appears to be an early ribbed offshoot of the main stricklandiid line; a parallel development is seen in *Costistricklandia*, which appeared toward the end of Upper Llandovery time (C_5 – C_6).

ONE of the specimens which Davidson included on his plate illustrating the species *Stricklandia lirata* was 'An internal cast of a small, exceptionally shaped or malformed specimen' collected from Nash Scar, near Presteigne (Davidson 1864–71, pl. 20, fig. 13). The specimen is preserved in the Geological Survey Museum and is unlike other stricklandiids in having very irregular, coarse, contorted costae. It might be considered an aberrant *Costistricklandia lirata*, but it was not a contemporary of *C. lirata*; this is indicated by the presence on the same block as the original specimen of several specimens of *Eocoelia* identical with Williams's subspecies *Eocoelia* (= *Coelospira*) *hemisphaerica sefiuensis* (Williams 1951, p. 113). This *Eocoelia* occurs in C_1 beds at Llandovery and evolved into another form which occurs in C_4 beds at Llandovery (op. cit., p. 129). An upper time limit of C_3 may thus be established for Davidson's specimen, whereas *Costistricklandia lirata* with costae of equivalent strength did not appear until C_6 of the Upper Llandovery (op. cit., p. 129; St. Joseph 1935, p. 421).

To resolve this problem, bulk collections were made from all the fossil localities at present exposed in the Upper Llandovery beds of the inlier near Presteigne (see Table 1). Stricklandiids are nowhere abundant at Presteigne, but a few specimens were discovered in five of the six samples collected; one of these samples (No. 10247) came from a sandstone outcrop above the limestone quarries at Nash Scar and is probably close to Davidson's locality. The Nash Scar collection yielded two pedicle valves similar to Davidson's specimen and two pedicle valves of the ordinary smooth *Stricklandia lens*. Specimens like Davidson's were also found at locality 10245, a mile to the east-north-east. Thus, several specimens of Davidson's peculiar stricklandiid are now known from two, possibly three, localities. At locality 10247 they occur together with the distinctly different smooth *Stricklandia lens*. A new name, *Aenigmastricklandia contorta*, is here proposed for the peculiarly ribbed and distorted species.

A second, but possibly related, problem is posed by the other three collections. They contain smooth specimens referred to *Stricklandia lens* aff. *progressa*, but the specimens are small for this species (2.5 cm. long at the most) and some have asymmetric indentations (Pl. 58, fig. 6). These specimens are thus similar in some respects to the new species, *Aenigmastricklandia contorta*, but they do not have costae of any sort, and they have very short hinge-lines in contrast to specimens of *A. contorta* which have hinge-lines

TABLE 1. Localities of the Presteigne stricklandiid collections

USNM No.	Field No.	Grid Ref.	Exposure	Location	Stricklandiids
10242	P-R-A	SO/3177 6343	loose blocks beside secondary road	125 yds. north of 'The Folly' and 275 yds. NW of Corton House.	<i>Stricklandia lens</i> aff. <i>progressa</i>
10243	P-Q-A	SO/3197 6334	very large disused quarry	North of the B4362 road across from Corton House and 170 yds. WSW of railway bridge.	<i>Stricklandia lens</i> aff. <i>progressa</i>
10244	P-N-C	SO/3160 6320	small disused quarry	North of the B4362 road about 1 mile ENE of Nash Scar and 690 yds. WSW of railway bridge.	<i>Stricklandia lens</i> aff. <i>progressa</i>
10245	P-N-D	SO/3153 6316	roadside exposure	North of the B4362 road about 1 mile ENE of Nash Scar and 690 yds. WSW of railway bridge.	<i>Aenigmastricklandia contorta</i>
10247	P-S-A	SO/3018 6234	slumped outcrop	Above the large limestone quarries at Nash Scar.	<i>Aenigmastricklandia contorta</i> <i>Stricklandia lens</i>

that form, in some cases, the maximum width of the shell. The cardinalia are also different; the specimens referred to *S. lens* aff. *progressa* possess outer plates, but these are absent in the one brachial valve available of *A. contorta*. Thus, the specimens referred to *S. lens* aff. *progressa* are quite distinct from *A. contorta* despite some superficial similarities.

SYSTEMATIC DESCRIPTION

Genus *Aenigmastricklandia* nov.

Type species. Aenigmastricklandia contorta gen. et sp. nov.

Diagnosis. Aenigmastricklandia is a small stricklandiid characterized by very coarse irregularly branching costae and by a deep fold in the brachial valve with corresponding sulcus in the pedicle valve.

Comparison. Aenigmastricklandia differs from its contemporary, *Stricklandia*, in having costae and in having the 'outer plates' of the cardinalia atrophied; and from *Costistricklandia* in the irregularity of its costae, the prominence of its fold and sulcus, and the width of its hinge-line.

Aenigmastricklandia contorta gen. et sp. nov.

Plate 58, figs. 8-16

Holotype. Stricklandia lirata pars. Davidson 1864-71, 159-61, pl. 20, fig. 13, but not figs. 1-12.

Description. Exterior. The pedicle valve is quite convex and the brachial valve less so. The length-width dimensions are about equal, the greatest width being at the hinge-line

or just anterior to it. A prominent, rather narrow fold is present in the brachial valve with a corresponding sulcus in the pedicle valve. Commonly, there are irregular folds on other parts of the valves. Coarse uneven costae cross the valves and branch irregularly.

Interior of brachial valve. Only one specimen is known. It possesses cardinalia of a type reminiscent of *Stricklandia lens ultima* and *Costistricklandia lirata*; that is, the 'outer plates' are atrophied, and the 'inner plates' occur laterally to the brachial processes (Williams 1951, p. 103).

Interior of the pedicle valve. A spondylium is present but the median septum is atrophied.

Distribution. This species is known only from two localities (10245 and 10247) from the early Upper Llandovery beds of the small inlier to the south of Presteigne, Radnorshire.

Genus *Stricklandia*

Stricklandia lens aff. *progressa* Williams 1951

Plate 58, figs. 1-7

Description. Exterior. The pedicle valve is more convex than the brachial valve. The valves are often pear-shaped; the hinge-line is very short and the valve expands anteriorly. A fold is usually developed in the brachial valve with a corresponding sulcus in the pedicle valve. Some valves are not symmetrical and may have irregular folds or indentations.

Interior of brachial valve. The cardinalia are as figured by Williams (1951, pl. 5, figs. 1-3); outer plates, inner plates, and brachial processes are developed.

Interior of pedicle valve. The spondylium is present as usual and is supported by a short median septum.

Comparison. *Stricklandia lens* aff. *progressa* from Presteigne is similar to specimens from the type locality of *S. lens progressa* at Mandinam, Llandovery district (Williams

EXPLANATION OF PLATE 58

All figures $\times 2$. USNM—United States National Museum; GSM—Geological Survey and Museum.

Figs. 1-7. *Stricklandia lens* aff. *progressa* Williams.

1, 2, USNM Collection No. 10244, spec. 140421; 1, Posterior view of internal mould of brachial valve; 2, Internal mould of brachial valve.

3, 4, USNM Collection No. 10244, spec. 140422; 3, Posterior view of internal mould of brachial valve; 4, Internal mould of brachial valve.

5, 6, USNM Collection No. 10244, spec. 140423; 5, Posterior view of internal mould of brachial valve; 6, Internal mould of brachial valve.

7, USNM Collection No. 10243, spec. 140424; Internal mould of pedicle valve.

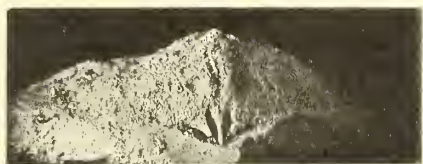
Figs. 8-16. *Aenigmastricklandia contorta* gen. et sp. nov.

8, 9, USNM Collection No. 10245, spec. 140425; 8, Posterior view of internal mould of brachial valve; 9, Internal mould of brachial valve.

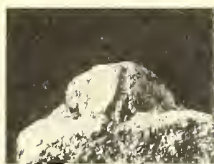
10-13, USNM Collection No. 10245, spec. 140426; 10, Posterior view of rubber replica of exterior of pedicle valve; 11, Rubber replica of exterior of pedicle valve; 12, Internal mould of pedicle valve; 13, Anterior view of internal mould of pedicle valve.

14, USNM Collection No. 10247, spec. 140427; Posterior view of rubber replica of exterior of pedicle valve.

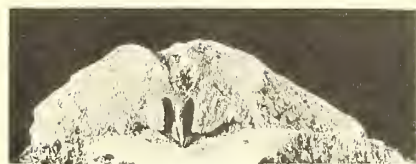
15, 16, Holotype, GSM 13783, Nash Scar, Presteigne; 15, Internal mould of pedicle valve; 16, Anterior view of internal mould of pedicle valve.



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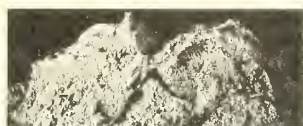
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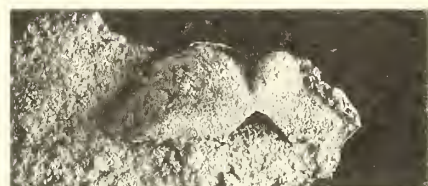
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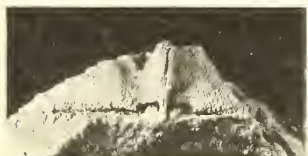
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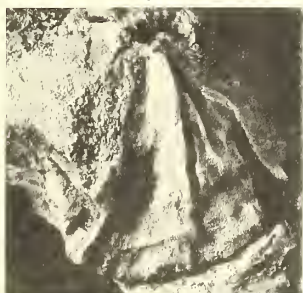
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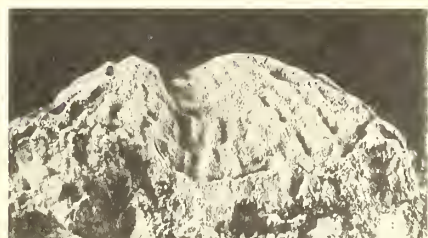
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16

1951, p. 102), but the specimens are only about half as long, with irregularities in the growth of the valves, and the hinge-line is unusually short.

Distribution. At Presteigne, *S. lens* aff. *progressa* occurs at localities 10242, 10243, and 10244 and possibly at locality 10247.

Conclusions

There are at least three ways to account for one or both of the unusual stricklandiids at Presteigne: (1) the individuals may have been diseased; (2) they may have been the victims of particularly harsh environmental conditions; or (3) they may have become genetically distinct from the parent stock, *Stricklandia*. The rocks are not deformed in any way, so the possibility that the specimens were contorted after they were buried may be ruled out. The first possibility is considered the least likely; a disease probably could not have produced the strong ribs of *Aenigmastricklandia*, and though it might have caused the deformities common among the stricklandiids described, it would be necessary to assume that this disease was peculiar to Presteigne, and persisted for some time (Collection 10245 came from at least 25 ft. stratigraphically above Collection 10244).

The second possibility, that of harsh environmental conditions, must be examined carefully. The fact that the stricklandiids of Presteigne are rare, small, and usually deformed suggests that environmental conditions unfavourable to stricklandiids persisted. The situation at Presteigne is particularly marked when compared with some surrounding areas, where large individuals of *Stricklandia* occur in profusion and characteristically dominate the faunal assemblage. An example of an environmental condition that might have caused the deformities in the stricklandiids of Presteigne is fast current action; there is, in fact, a suggestion in the conglomeratic nature of the sandstones that strong current action persisted at Presteigne. Under such conditions the mantles of the stricklandiids might very well have become damaged, resulting in the asymmetric, irregular form of the valves.

Environmental extremes are sufficient to account for many of the features of the Presteigne stricklandiids, but *Aenigmastricklandia* possesses a variety of characters, such as a prominent fold and sulcus, a wide hinge-line, and coarse costae, which easily distinguish it from contemporary stricklandiids and point to an evolutionary history separate from the main *Stricklandia lens* community. Alternatively, *Aenigmastricklandia* may have been a sport, but it was clearly viable since several specimens are known. In either case, *Aenigmastricklandia* would have been genetically distinct from *Stricklandia*.

In conclusion, the Upper Llandovery rocks of Presteigne are thought to represent a difficult environment for stricklandiid brachiopods. Two distinct genera, *Stricklandia* and *Aenigmastricklandia*, did, however, survive there, though specimens of each show deformities. Probably the individuals referred to *S. lens* aff. *progressa* drifted, as larvae, into the area from neighbouring *S. lens* *progressa* communities and either died in their youth or became stunted. *Aenigmastricklandia*, on the other hand, may have been endemic to the environment represented at Presteigne where it may very well have had an evolutionary history separate from the common *S. lens* community.

In any case, the presence of coarsely ribbed stricklandiids in deposits which may be confidently dated as early Upper Llandovery (C₁-C₃) on the basis of *Eocoelia hemisphaerica sefinensis* and *S. lens* aff. *progressa* must induce a measure of caution in those

concerned with correlating Silurian deposits. Up to now it has been assumed that the occurrence of strongly ribbed stricklandiids indicated a late Upper Llandovery age (C₆), particularly as *Costistricklandia lirata typica* St. Joseph (C₆) may be linked with *Stricklandia lens ultima* Williams (C₄) by a series of forms showing intermediate grades of rib strength; these intermediates find taxonomic expression in the subspecies *Costistricklandia lirata alpha* St. Joseph. The development of ribbing in stricklandiids evidently occurred more than once.

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THE FINE STRUCTURE OF SOME LOWER TRIASSIC ACRITARCHS

by ALAN WILLIAM MEDD

ABSTRACT. Acritarchs from the Lower Triassic of Western Australia are examined with an electron microscope. As they are almost opaque to the electron beam, a modified replication technique is used to elucidate the fine structure of their tests. This examination is shown to be of taxonomic value, and a new variant is described.

THE electron microscope has proved a very useful tool in the study of foraminifera (Hyde and Krinsley 1964), pollen (Pettit and Chaloner 1964), and coccoliths (Black and Barnes 1961; Black 1963). The present paper describes its application to the acritarchs. Examination of their replicas shows the presence or absence of even the smallest structure on the surface of the acritarch test. Such an examination, together with one using an optical microscope, has led the writer to revise several species of Triassic acritarchs.

Material. This paper is based on a sample (No. 43305) of Lower Triassic (Scythian), prepared by Balme (1963), from the Kockatea Creek No. 19 Bore, over 300 miles north of Perth, Western Australia. The sample is rich in excellently preserved microfossils, particularly the acritarchs.

All the specimens and photographs described are now in the Archive Collection of the Department of Geology, University of Reading.

Methods. Some of the material was mounted in glyccrin jelly on glass slides and then examined with an optical microscope.

A dilute suspension of this sample was dried on a Formvar membrane, which rested on a 200 mesh-to-the-inch copper grid. The sample was then examined with a Philips EM75C electron microscope. As the acritarchs are almost opaque to electrons, a satisfactory transmission-electron image of their surface detail can only be obtained when the condenser lens is set for maximum intensity. Unfortunately, the heat generated by the electron bombardment of the Formvar membrane at this intensity is such as to break the membrane. Therefore, a lower electron intensity must be used and this is seldom found to produce satisfactory micrographs because of the loss of most of the surface detail (Pl. 59, fig. 1).

Replica techniques overcome this problem as the carbon film, which has been deposited on the specimen, exactly reproduces the surface detail and is stable under electron bombardment. The method, adopted by Bradley and Williams (1957) for the study of spore morphology in the genus *Bacillus*, is followed here with some refinements of their technique. The carbon film may break when the specimen is dissolved, as there is a slight swelling of the specimen and also because the solvent slowly attacks both carbon and copper. Other replica techniques have been developed to overcome these problems (Bradley 1958; Takeoku and Stix 1963), but repeated attempts to use these techniques on the acritarchs failed to obtain more than a few satisfactory replicas of the commonest species in the assemblage.

If the specimen is coated with a single thickness of carbon of 250–400 Å, instead of 100–200 Å as recommended by Bradley, the extra thickness of film renders it more resilient to the later chemical processes. It should not be so thick, however, as to mask the finer surface detail. The solvent used is a freshly made 20% solution of potassium dichromate and potassium permanganate mixture in concentrated sulphuric acid, instead of the 10% solution as used by Bradley. The grid is slowly immersed in this solution and held there in a vertical position for only a few seconds. The grid is then removed and washed first in dilute sulphuric acid, and then in concentrated hydrochloric acid, 50% hydrochloric acid, 10% hydrochloric acid respectively, and finally twice in distilled water. After drying it is

ready for shadowing with platinum/palladium metal. With this series of washings after the solvent treatment, there is usually a high percentage of the grid still covered by the film, and so every species in the assemblage can be examined with the electron microscope. Electron micrographs were taken on Ilford N60 plates and developed in Kodak D76.

SYSTEMATIC DESCRIPTIONS

Group Incertae sedis ACRTARCHA Evitt 1963

Sub-group SPHAEROMORPHITAE Downie, Evitt and Sarjeant 1963

Genus MICRHYSTRIDIUM Deflandre 1937 emend. Downie and Sarjeant 1963

Micrhystridium cf. *breve* Jansonius 1962

Plate 59, fig. 6

Remarks. Electron micrographs of the specimens referred to this species show that the thin-walled test possesses large, irregularly arranged granules; the processes are short (length about 2μ) and are easily broken, when they leave bosses (diameter 0.5μ) on the surface of the test. Although the specimens examined have a smaller test diameter (about 11μ) than that considered to be typical by Jansonius, they are otherwise similar to one of his figured specimens: Imp. 3010–2–113.5 $\times$ 28.6.

Micrhystridium cf. *fragile* Deflandre 1947

Plate 59, figs. 1 and 2a, b

Remarks. The electron micrographs show that the test and processes are thin-walled and are covered by a regular arrangement of small granules (diameter about $500\text{ \AA}$). The long processes of this species are robust but flexible and occasionally develop from expanded bases on the surface of the test.

Wall and Downie (1963) suggest that the only valid criteria for distinguishing *M. fragile* Deflandre from *M. stellatum* Deflandre are that the former has delicate processes without expanded bases, and that the latter possesses relatively rigid processes whose bases are expanded. The Triassic specimens examined have some of the diagnostic elements of both species: they have a test diameter of about 13μ (about $25\text{--}29\mu$ including processes), which is comparable to the range of measurements of *M. stellatum* as given by Wall and Downie. The occasional basal expansion of the processes is also characteristic of *M. stellatum*, whereas the dominantly spherical nature of the test and the flexible processes are diagnostic of *M. fragile*. Wall and Downie also stated that: 'Separation of the two species becomes artificial to some extent, especially in some

EXPLANATION OF PLATE 59

Figs. 1, 2a, b. *Micrhystridium* cf. *fragile* Deflandre. 1, E.M. 213, $\times 3500$. 2a, E.M. 291, $\times 3000$. 2b, E.M. 291, showing the granular test surface, $\times 10,000$.

Figs. 3–5. *Veryhachium reductum* (Deunff) Jekhowsky. 3, Forma *breve*, E.M. 250, $\times 3300$. 4, Forma *trispinoides*, E.M. 204, $\times 2500$. 6, Form with a coarsely granular test, E.M. 777, $\times 3200$.

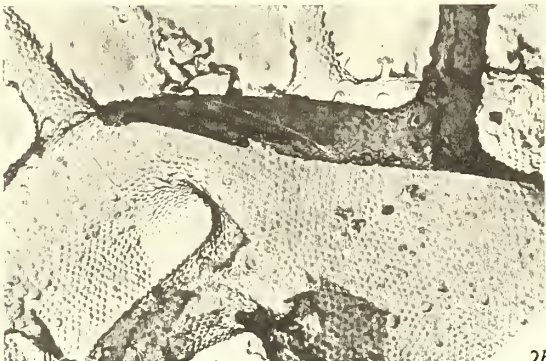
Fig. 6. *Micrhystridium* cf. *breve* Jansonius, E.M. 260, $\times 5000$.

Figs. 1 and 4 are electron micrographs of the specimens; figs. 2a, b, 3, 5, and 6 are carbon replicas shadowed at 45° with platinum/palladium.

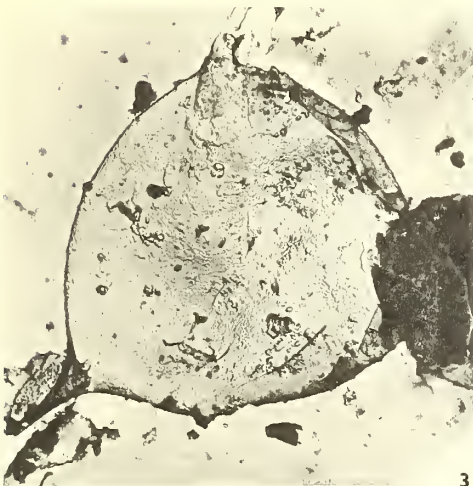


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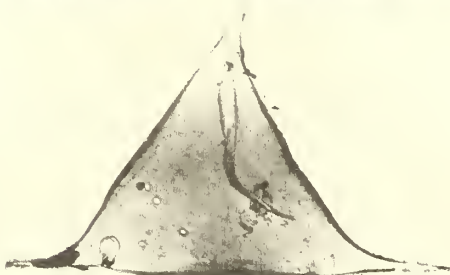
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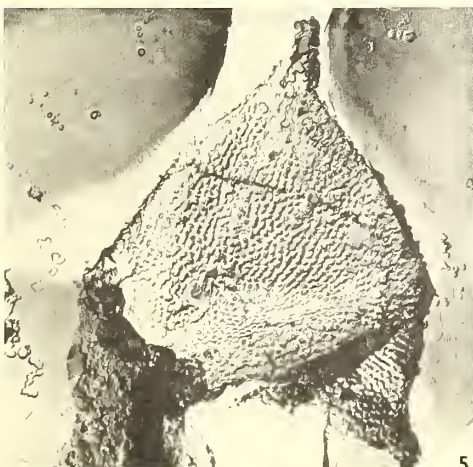
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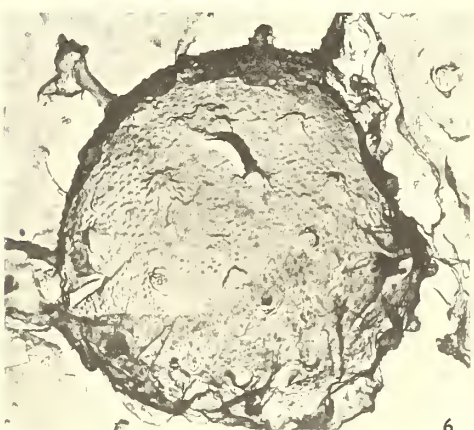
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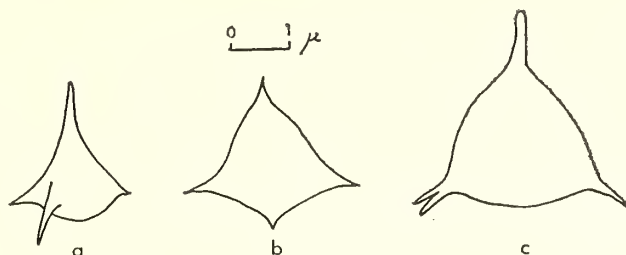


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6

Jurassic strata, but on this basis the Permian forms must be regarded as belonging to *M. stellatum* since their spine bases are always expanded even if the spines are not always rigid.' Agreeing with these remarks, the writer by contrasted reasoning considers the Triassic specimens to belong to *M. fragile*; forms comparable with the holotype of *M. stellatum* are not found in this sample.



TEXT-FIG. 1. *Veryhachium reductum* Deunff, forms possessing a fourth process.
a, S.A.M. 1-67 $\times$ 152. b, S.A.M. 2-54 $\times$ 119. c, S.A.M. 3-210 $\times$ 151.

Sub-group POLYGONOMORPHITAE Downie, Evitt and Sarjeant 1963
Genus VERYHACHIUM Deunff 1954, emend. Downie and Sarjeant 1963

Veryhachium reductum Deunff 1954

Plate 59, figs. 3-5; text-fig. 1

Remarks. All of the morphological variants described by Jekhowsky (1961) can be recognized in the sample, and there is no dominance of any of his types. Electron micrographs show the test to be thin-walled and to have a surface irregularly covered by fine granules. A further morphological variant which is occasionally found in the sample has a coarsely granular test with convex sides, together with three short processes. This is differentiated from *V. reductum* forma *breve* Jekhowsky by the more granulose nature of the test. Although this is suggested by the optical microscope investigation, it is clearly shown by the electron micrographs.

During an optical examination of several hundreds of specimens of this species, four were found to possess four processes instead of the typical three. One of the corner processes is bifid in two examples (text-fig. 1c), and they are probably similar to the type mentioned by Brosius and Bitterli (1961) for a specimen from the Trochitenkalk (Upper Muschelkalk). The other two have a fourth process on a separate part of the test, and all four processes are approximately of the same size.

Examination with an optical microscope of the tests of many specimens shows that their surface is often irregular. The electron micrographs indicate that there is some irregular folding of the test wall in about 40 per cent. of the specimens. This folding can occur anywhere on the test, perhaps with breakage of the test wall. Such folding and tearing occurs in other species in this sample, and could be interpreted as being collapse structures, caused by the compaction of the sediment.

Jansonius (1962) stated that: 'In Australian samples of Lower Triassic age forms assignable to *Wilsonastrum* occur abundantly; these have in part a modest but distinctive ornamentation, and show the tiny bristle very clearly. These include specimens

of *W. colonicum* n. sp.' None of the specimens of this sample, examined with either the optical or the electron microscope, reveals the presence of this bristle, and so forms of the genus *Wilsonastrum* Jekhowsky are absent from this sample.

Acknowledgements. The writer thanks Mr. B. E. Balme for his help and for the opportunity to examine sample No. 43305 from the collection of the Department of Geology, University of Western Australia, and to Mr. D. B. Williams for helpful discussion during the preparation of the manuscript. The work was made possible by the award of a B.P. research grant.

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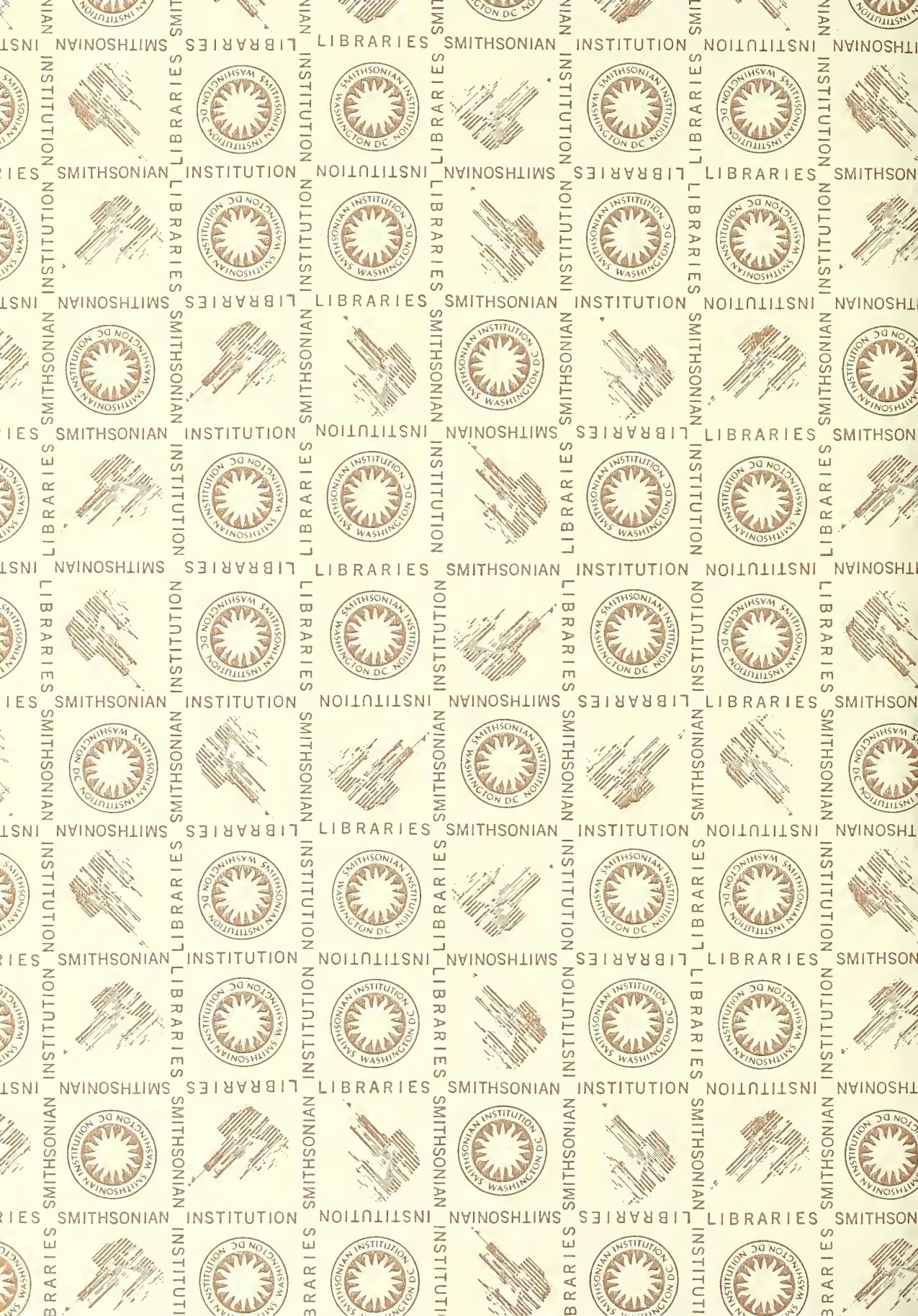
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